Mechanisms and consequences of variation in the migratory behaviour of Atlantic cod (*Gadus morhua* L.) in the northern Gulf of St. Lawrence.

by

© Arnault Le Bris

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ABSTRACT

This thesis aimed to characterize individual variation in the migratory behaviour of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence, and to assess the consequences of this variation on the structure and management of the population. First, I reviewed interplays between genetic, environmental, and social factors in the evolution and maintenance of individual variation in the migratory behaviour of marine fishes, with an emphasis on Atlantic cod. Evidence of fine-grained responses to environmental changes suggested that phenotypic plasticity is a substantial source of variation in migratory behaviours. However, because the genetic basis of migratory traits has been overlooked, the relative contributions of genetic, environment, and genetic by environment interactions have not been quantified for any marine fishes. Within the cod population from northern the Gulf of St. Lawrence, reconstruction of migration routes of cod equipped with data-storage tags revealed undocumented concurrent presence of resident and migratory individuals. Depth time-series analyses revealed high individual variability in vertical patterns of migration. Consequences of the observed individual variation in migration propensity on the structure of the population were then evaluated. Focusing on the fjord of Bonne Bay where I previously identified resident and homing cod, I assessed the degree of demographic dependency of Bonne Bay cod with Gulf cod. Although local recruitment occurs, Bonne Bay does not harbour an abundance of adult cod and external sources of recruitment are substantial. The bay however provides a

nursery and a spawning area for Atlantic cod. Finally, I quantified effects of variation in adult migratory behaviour and population density distribution on the performance of a fishery closed area designed to protect a spawning aggregation. Closed area usage by free-ranging individuals revealed disproportional levels of protection between migratory groups. Estimated population density distributions during two periods of contrasted abundance level suggested that, when a closed area is located on the core of a population distribution, density-dependent contraction of population range increases closed area performance. Both individual closed area usage and population density distribution indicated that a displacement south and a reduction of the enforcement period would improve the performance of the study closed area.

RÉSUMÉ

Cette étude a visé à caractériser les variations individuelles du comportement migratoire de la morue franche (*Gadus morhua*) du nord du golfe du Saint-Laurent, ainsi qu'à évaluer les conséquences de ces variations pour la structure et la gestion de la population. Dans un premier temps, les rôles respectifs des facteurs génétiques, environnementaux et sociaux dans l'évolution et le maintien d'une variabilité individuelle du comportement migratoire des poissons marins, et notamment de la morue franche, ont été revus. Les réponses aux changements du milieu ont suggéré que la plasticité phénotypique contribue substantiellement à la variation observée dans le comportement migratoire des poissons marins. Cependant, étant donné que les facteurs génétiques n'ont pas été évalués, les contributions relatives du génotype, de l'environnement, et des interactions génotype -

environnement n'ont été quantifiées pour aucune espèce des poissons marins. Au sein de la population de morue du nord du golfe du Saint-Laurent, la reconstruction des parcours migratoires d'individus équipés d'étiquettes électroniques enregistreuses a révélé la présence d'individus résidents et d'individus migrateurs. De plus, l'analyse de séries temporelles de profondeur a montré une grande variabilité intra et interindividuelle dans les patrons de migration verticale. Les conséquences de la variabilité de la tendance à migrer pour la structure de la population ont ensuite été évaluées. En se concentrant sur le fjord de Bonne Baie où des individus résidents et un comportement de homing ont été identifiés, cette étude a évalué la dépendance démographique de la morue de Bonne Baie vis-à-vis de la morue du golfe. Bien que du recrutement local apparaît, aucune population ne vit actuellement dans Bonne Baie. La baie constitue cependant une nourricerie et une frayère pour la morue du golfe. Enfin, les effets de la variabilité du comportement migratoire et de la densité de distribution de la population sur la performance d'une zone de fermeture de pêche ont été quantifiés. Les fréquentations individuelles de la zone de fermeture ont révélé des niveaux de protection inégaux entre les deux groupes migratoires précédemment identifiés. Les estimations de densités de population durant deux périodes d'abondance contrastée ont suggéré que des changements densité-dépendant de la distribution d'une population augmentent l'efficacité des zones de fermetures placées au cœur de la distribution de la population. Les fréquentations individuelles et les densités de distribution ont également suggéré qu'un déplacement de la zone de fermeture vers le sud ainsi qu'une réduction de sa durée augmenterait son efficacité.

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Arnault Le Bris

St. John’s, Newfoundland, June 21, 2014

À Pierro. J'aurais aimé partager l'aboutissement de ce travail avec toi. RIP my friend.

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Symbols	
$\Phi\ (\mu, \sigma)$	Normal cumulative distribution function with mean μ and variance σ
$\varphi(\boldsymbol{x}, t)$	Probability density function of the fish position $\boldsymbol{x}(x, y)$ at time t
β	Model coefficient
ε	Residual error
θ	Tidal phase
$\boldsymbol{\theta}$	Vector of parameters
ω	Angular frequency
τ_x / τ_y	East-West and North-South wind stress
A	Tidal amplitude
B	Biomass
C	Catch
d	day
D	Diffusion coefficient
df	degrees of freedom
F_{IS}	Within sample heterozygote deficit
F_{ST}	Fixation index
Ho / He	Observed and expected sample heterozygosity
K	Carrying capacity
maxz / minz	Daily maximum and minimum depth recorded by tag
N	Abundance
Pan I	Pantophysin locus
r	Growth rate
SPI / TPI	Spatial and temporal performance index
tp	Temperature
z	Depth

Abbreviations

AIC	Akaike Information Criteria
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CT	Conventional Tagging
CTD	Conductivity Temperature Depth
DFO	Department of Fisheries and Oceans
DSTs	Data-Storage Tags
nDVM	normal Diel Vertical Migration
rDVM	reverse Diel Vertical Migration
ET	Electronic Tagging
FAO	Food and Agriculture Organization of the United Nations
FFAW	Fish, Food and Allied Workers
FL	Fork Length
FRCC	Fisheries Resource Conservation Council
GLM	General Linear Model
nGSL	northern Gulf of St. Lawrence
HMM	Hidden Markov Model
MAPAQ	Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec
MLE	Maximum Likelihood Estimation
MCMC	Markov Chain Monte Carlo
NAFO	Northwest Atlantic Fisheries Organization
PSATs	Pop-Up Satellite Archival Tags
RMSE	Root Mean Square Error
SD	Standard Deviation
SL	Standard Length
SNPs	Single Nucleotide Polymorphisms
SSM	State-Space Model
TLM	Tidal Location Method

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Chapter 1. Introduction and Overview

1.1. Introduction

1.1.1. Variation in migratory behaviour

Variation in marine fish migratory behaviour is more prevalent among and within populations than previously recognized (Ruzzante et al., 2006; Chapman et al., 2012b). Increased evidence on its evolutionary and ecological significance (Jørgensen et al., 2008; Chapman et al., 2012a), as well as on its consequences for the assessment, management and conservation of populations (Cadrin and Secor, 2009; Svedäng et al., 2010; Grüss et al., 2011b), have underlined the need for its careful characterization in order to exploit sustainably marine fisheries resources. In this thesis, I investigate whether variation in the migratory behaviour of the collapsed population of Atlantic cod *Gadus morhua* L. 1758 from the northern Gulf of St. Lawrence is more complex than currently documented, and whether this variation affects the spatial structure of the population and the performance of spatiotemporal management measures.

From an evolutionary perspective, the study of variation in animal migration has helped understand how genetic and environment interplay in shaping phenotypes (Dingle, 1996; Liedvogel et al., 2011), and helped reveal rates of phenotypic responses to changing selective pressures (Berthold et al., 1992; Westley, 2011). The respective roles of genetic, environmental, and social factors in the evolution and maintenance of

individual variation in the migratory behaviour of marine fish species remains however mysterious, especially in comparison to that of other animal taxa such as insects, birds, and salmonid fishes (Roff and Fairbairn, 2007; Pulido and Berthold, 2010; Dodson et al., 2013). In light of current changes in the oceanographic environment, it is fundamental to understand the degree to which genetic, environmental, and social sources of variation interplay in shaping marine fish migratory behaviours if one wants to predict future distribution of marine fish populations (chapter 2).

Ecological causes of variation in migratory behaviours have long been identified (Harden Jones, 1968; Leggett, 1977; Northcote, 1978) and the ecological consequences start to be understood. Variation in migration timing and propensity affects productivity, stability and resilience of populations and population complexes (Hilborn et al., 2003; Kerr et al., 2010; Schindler et al., 2010). Variation in dates of arrival on feeding areas and in the ratio of migrants to residents alters community composition and ecosystem processes at lower trophic levels (Post et al., 2008; Brodersen et al., 2011). These ecological consequences highlight the need to characterize variation in marine fish migratory behaviour and habitat preferences (chapter 3).

A widely documented consequence of variation in migratory behaviour is the formation of complex population structure. Site fidelity and homing behaviour to isolated spawning areas induce spatial segregation of spawning groups (Green and Wroblewski, 2000; Robichaud and Rose, 2001). In combination with mechanisms that facilitate

retention or return of spawning products to their natal area (Cowen et al., 2000; Thorrold et al., 2001), segregation of spawning groups may reduce gene flow and lead to the formation of local populations (Ruzzante et al., 2000b; Hauser and Carvalho, 2008). Differential selective forces resulting from gradients in the environmental conditions experienced by local populations may then generate variation in life-history traits among local populations (Conover et al., 2006; Nielsen et al., 2009a). As most stock assessment models and fishery management plans critically assume homogenous vital rates (Brêthes, 1990; Hilborn and Walters, 1992; Cadrin et al., 2004), formation of small scale population structures may result in erroneous stock assessments and inefficient management plans, which often place the most accessible and less productive local populations at risk of extirpation (Smedbol and Stephenson, 2001; Svedäng et al., 2010). Evaluating the potential for population structure resulting from variation in migratory behaviour (chapter 4) is thus essential to developing spatially explicit stock assessment models and to match scales of population structure and management units (Cadrin and Secor, 2009; Reiss et al., 2009).

Variation in migration not only affects population structure, but also challenges the performance of spatiotemporal management and conservation measures, such as the creation of marine protected areas and the implementation of fishery closures (Horwood et al., 1998; Gell and Roberts, 2003; Grüss et al., 2011a). The performance of closed areas designed to protect migratory populations depends upon the size and location of the areas with respect to populations' distributional range, the extent of individual movement

across closed area boundaries, and the fishing intensity in adjacent areas or in periods preceding and following seasonal closures implementation (Murawski et al., 2000; O'Boyle, 2011). The larger the distributional range of a population is relative to a closed area size, the less likely will the closed area help in ensuring persistence of the exploited population (Claudet et al., 2008; Moffitt et al., 2009). Contraction in population distributional ranges caused by either density-dependent or -independent factors may affect the performance of a closed area (Guénette et al., 1998). Alternative migratory behaviours within a population may lead to differential levels of protection among migratory types. For instance, individuals displaying site-fidelity within a closed area will benefit from a maximal level of protection, while highly migratory individuals will be protected only during periods of transit through the closed area. Quantification of individual variability in closed area usage and monitoring of changes in population distributional range are thus necessary to find the optimal design (*i.e.* size, location, and enforcement period) of a closed area (chapter 5). Finding closed area optimal design helps the sustainable management of fisheries resources. Excessively large and prolonged closures may diminish harvesters' compliance with regulations and increase enforcements costs, while too small, too short, and not appropriately located closures may not offer sufficient protection to exploited populations (FAO, 2011).

1.1.2. Using electronic tags to study fish migration

Marine systems have long suffered from difficulties to observe individuals in their natural environments. Early studies on fish migration relied on catch data and conventional mark-recapture experiments to identify general migration routes (Hjort, 1914; Templeman, 1979). Unfortunately, these methods provide snapshots of fish position that are often biased by fishing effort and regulations, thus impeding detailed understanding of individual migratory behaviour at fine spatiotemporal scales. Recent technological advances in data collection equipment and in analytical and quantitative approaches have revolutionized the study of fish migration from fishery independent observations. Acoustic tags are increasingly used to characterize behavioural patterns such as spawning site fidelity (Green and Wroblewski, 2000; Topping et al., 2006; Skjæraasen et al., 2011), multiyear homing (Robichaud and Rose, 2001), and closed area usage (Meyer et al., 2000; Afonso et al., 2009; Siceloff and Howell, 2013). The limited listening range of hydrophones and acoustic receivers implies that acoustic tags are primarily used for micro-scale studies (10s of km) unless large arrays of receivers are deployed (Comeau et al., 2002b; Heupel et al., 2006; Brattey et al., 2008).

With the recent improvements in battery life and memory capacity, archival tags (*i.e.* pop-up satellite tags, PSATs, and data-storage tags, DSTs) recording environmental variables during fish migration provide new opportunities to characterize fish migratory behaviour and habitat preferences over long distance and continuous time (Sims et al.,

2008; Righton et al., 2010; Block et al., 2011). An inherent limitation of archival tags is the lack of direct observations of fish locations. Locations need to be inferred from the recorded environmental variables, the so-called geolocation problem (Evans and Arnold, 2009; next section). While PSATs do not need physical recapture to access the data, their size and price limit their use to large commercial pelagic species (although new miniature PSATs are now used to track eel and cod; Aarestrup et al., 2009; Rose et al., 2013). On the contrary, DSTs need physical recapture to access the data, but their size and price allow study of smaller species and ability to tag a larger number of individuals. Because of the size of adult cod in the northern Gulf of St. Lawrence relative to the size of the technology available in 2007 at the beginning of the electronic tagging program, and because of the scale of the study area, DSTs were used in this thesis to characterize individual variation in the migratory behaviour of Atlantic cod in the northern Gulf St. Lawrence.

1.1.3. The geolocation problem

Before introducing the study population and the objectives of this thesis, an explanation of the geolocation problem is necessary to understand the challenge faced to reconstruct migration routes of cod equipped with DSTs in the Gulf of St Lawrence. When using archival tags, fish locations need to be inferred from recorded environmental variables (*e.g.* light intensity, depth, temperature, salinity). Light is the most convenient variable to geolocate fish. Light intensities recorded with light sensors reveal day-length and local

noon and midnight, which are in turn used to infer latitude and longitude, respectively. Errors in light-based geolocations are frequent due to changes in cloud cover, water turbidity, light attenuation with depth, proximity to the equator or to the poles, and temporal proximity to equinox (Musyl et al., 2001). State-space models (SSM, Appendix A) are thus used to remove outliers and refine location estimates. A widely used SSM to geolocate large pelagic fish based on light levels is the Kalman filter (Sibert et al., 2003), which can be extended with sea-surface temperature (Nielsen et al., 2006).

For demersal fish species that spent a significant amount of time near or on the sea-floor, the tidal signal can be extracted from the depth time-series recorded with tags. Phase and amplitude of the extracted tidal signal are compared with oceanographic tidal model to infer fish locations (the tidal location method; Metcalfe and Arnold, 1997; Hunter et al., 2003a). SSM are then used to join successive tidally inferred locations and remove spurious locations caused by multiple amphidromic points (point of zero fluctuation for one tidal consitutent) or by the extraction of low quality tidal information (Pedersen et al., 2008). Unfortunately, applications of the tidal location method are limited to areas with large tidal amplitude and a complex amphidromic system (tidal system with multiple amphidromic points), and to periods when fish are close to the seafloor. Low tag recording frequency and resolution can also impede the use of the tidal location method (Appendix B).

When neither direct observations of fish location, nor light intensities, nor tidal information are available, depth, temperature and salinity are compared with bathymetric, temperature and salinity grids to identify fish locations (Adlandsvik et al., 2007; Neuenfeldt et al., 2007; Righton and Mills, 2008). SSM can be used to improve track estimations significantly (Andersen et al., 2007; Thygesen et al., 2009). In this thesis, a combination of DSTs equipped with light, pressure and temperature sensors, and DSTs equipped with pressure and temperature sensors only were used. Unfortunately, no DSTs equipped with light sensors were recovered. The low tidal range in the Gulf of St. Lawrence prevented the use of the tidal location method (Appendix B). Therefore, I used a SSM implemented with depth and bottom temperature to reconstruct migration routes of Atlantic cod in the northern Gulf of St. Lawrence (chapters 3 and 5).

1.1.4. The northern Gulf of St. Lawrence Atlantic cod population

Similar to numerous demersal fish stocks in the northwest Atlantic, the northern Gulf of St. Lawrence (nGSL) Atlantic cod stock (Northwest Atlantic Fisheries Organization divisions 3Pn, 4RS) collapsed in the late 1980's and early 1990's. This collapse, induced by overexploitation (Hutchings and Myers, 1994; Myers et al., 1996a; Myers et al., 1996b; Sinclair and Murawski, 1997), and environmentally-driven decline in growth, reproduction, and survival (Dutil et al., 1999; Dutil and Lambert, 2000; Lambert and Dutil, 2000), led to the implementation of two moratoriums (a first one from 1994 to 1996 and a second one in 2003), and to the designation of the population as "threatened"

by the Committee On the Status of Endangered Wildlife in Canada (COSEWIC, 2003). Despite two decades of restricted fishing effort, a ban of fish trawling in the northern Gulf, the implementation of a fishery closed area to protect the main spawning aggregation, and an improvement in fish condition (Lambert, 2011), the stock has not recovered and is still considered well below conservation limit reference points (DFO, 2012). COSEWIC has recently suggested listing the population as "endangered" (COSEWIC, 2010). The demise of spawning components has been proposed as one hypothesis for the lack of recovery of the stock (Swain and Castonguay, 2000; Frank and Brickman, 2000; Smedbol et al., 2002; Yvelin et al., 2005).

General migration patterns have long been known for the population (NRC, 1899[1]; Templeman, 1979; Gascon et al., 1990; Yvelin et al., 2005). Cod overwinter outside the Gulf on the northern slope of the Laurentian Channel (Campana et al., 1999; Castonguay et al., 1999), migrate in spring to start spawning near St. George's Bay (Ouellet et al., 1997; Méthot et al., 2005) or near the Anticosti Island (Bui et al., 2011), and reach summer coastal feeding areas located along the west coast of Newfoundland, the Strait of Belle Isle, and the Québec North Shore (Figure 1.1). Whether fish use multiple migration routes used to reach the two main spawning grounds and the summer

[1]This historical report of the French fishery for cod along western Newfoundland classifies the fishery in two categories: 1) "la pêche nomade" (the nomadic fishery), in which boats follow cod migration up the coast, "migration caused by the migration of capelin shoals towards the Labrador coast", 2) "la pêche sédentaire" (the sedentary fishery) with fixed fishing station in Codroy (near Port-au-Basques), Red Island (St. George's Bay), and Port-au-Choix. The report interestingly mentions the presence of a winter fishery under the ice in Bonne Bay.

feeding grounds remains unclear (Figure 1.1), as does the possibility that some individuals do not display seasonal migration. Numerous ecological causes of variation in the population distribution have been identified, including temperature, depth, salinity (Castonguay et al., 1999; Ruppert et al., 2009; Tamdrari et al., 2012b), ice cover (Fréchet, 1990), prey distribution (Rose and Leggett, 1989), and population density (Tamdrari et al., 2010). However, variation in migratory behaviour at the individual level has been overlooked, and the consequences of such variation for the structure and the management of the population remain poorly understood.

The northern Gulf of St. Lawrence Atlantic cod stock (a group of individuals geographically delimited for management purposes) is managed as a unique population (a freely interbreeding group of individuals) and the structure of the population is poorly known. Conventional tagging and scale microchemistry analyses have suggested the existence of three subpopulations (Yvelin et al., 2005; Sagnol, 2007): i) the Anticosti subpopulation (4S); ii) the southwestern Newfoundland subpopulation (3Pn); and iii) the northeast Gulf subpopulation (4R). A subpopulation is an identifiable subset of a population, whose individuals share one or more common properties. The putative subpopulations in the nGSL were identified based on homing behaviour to summer feeding areas, while subpopulations are traditionally identified based on distinct spawning areas (McQuinn 1997, Smedbol and Wroblewski 2002, Wright *et al.* 2006). Accompanying the depletion of the population, the biomass has contracted in range along the west coast of Newfoundland (Ruppert et al., 2009; Tamdrari et al., 2010), but no study

has examined the distribution and abundance of cod in inshore waters along the west coast of Newfoundland, and especially the distribution of age-0 juvenile cod.

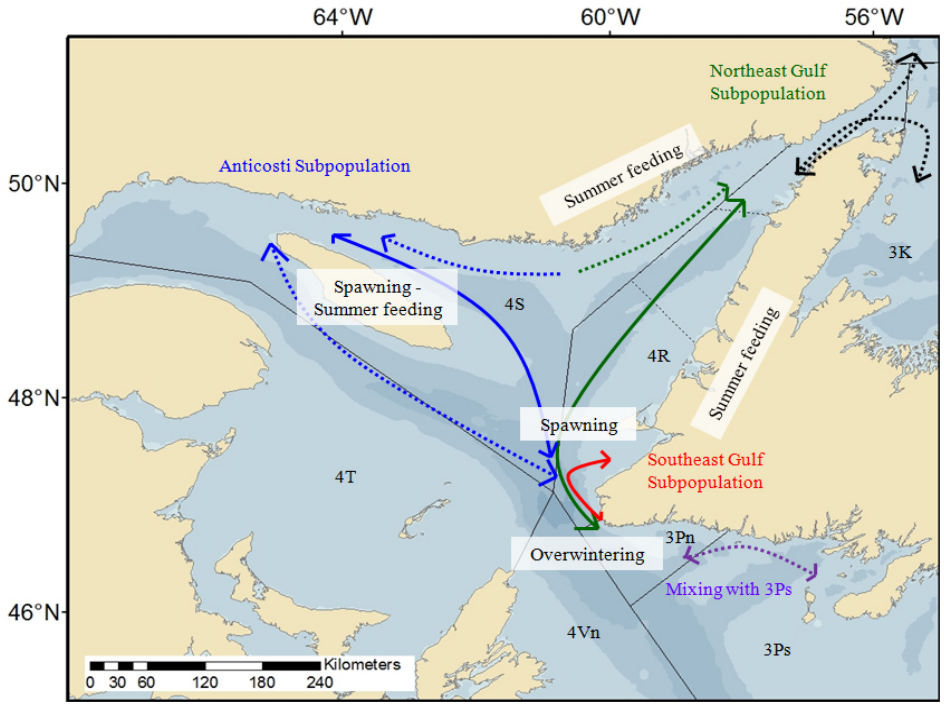

Figure 1.1. Atlantic cod migration routes, seasonal distribution areas, and putative population structure in the northern Gulf of St. Lawrence. Solid arrows: known migration routes. Dotted arrows: uncertain migration routes. Blue, green and red lines refer to the Anticosti, Northeast Gulf, and Southeast Gulf subpopulations, respectively (adapted from Yvelin et al., 2005). Black dotted lines show mixing possibilities with NAFO division 2J3KL, and purple dotted line shows mixing with NAFO division 3Ps.

1.2. Research objectives and overview

The global objective of this thesis was to advance knowledge on the mechanisms and consequences of variation in the migratory behaviour of marine fishes, and especially of Atlantic cod. This thesis focused on the collapsed population of Atlantic cod in the northern Gulf of St. Lawrence. During my research, I had four specific objectives:

1. To review the mechanisms of individual variation in the migratory behaviour of marine fishes and to identify current knowledge gaps.
2. To characterize the diversity of migratory behaviours in the nGSL Atlantic cod population using data-storage tags.
3. To assess the consequence of alternative migratory behaviours on the structure of the population.
4. To quantify the effects of individual variation in migratory behaviour on the performance of a fishery closed area.

In chapter 2, I review the mechanisms of individual variation in the migratory behaviour of marine fishes with a special emphasis on Atlantic cod. Evidence of the influence of phenotypic plasticity, genetic determinism, and social transmission on the migratory behaviour of marine fishes is reviewed. The need for new experimental protocols to quantify the genetic, environmental, and interactive (genotype by environment interactions) components of phenotypic variation in migration is examined. In chapter 3, I test the hypothesis that the nGSL Atlantic cod population comprises a mixture of resident

and migratory individuals. I explore two time-series analyses to reconstruct migration routes of cod equipped with data-storage tags, and to identify periodic behaviours indicative of resting, feeding, and spawning periods. In chapter 4, I examine the hypothesis that the observed site-fidelity of adult cod to Bonne Bay area leads to the formation of a local population. Abundance data from a 10 years long survey of the nearshore fish fauna of Bonne Bay is combined with environmental, fishery, maturity, and genetic data to assess the degree of demographic dependency of Bonne Bay cod with nGSL cod. Finally in chapter 5, I develop a methodology first to quantify the effects of individual variation in adult fish movement on the performance of fishery closed areas, and second to find the optimal design of fishery closed areas. Electronic tagging data are used to quantify fine-scale usage of a fishery closed area by free-ranging individuals. Conventional tagging data are used to obtain broad-scale population distribution patterns with respect to the fishery closed area. This new approach is applied to the spring fishery closed area designed to protect the main spawning aggregation of cod in the nGSL.

Early in my doctoral program I decided, in consultation with my thesis committee, to write a paper-based thesis rather than using a more traditional thesis format. An unfortunate consequence of this choice is the presence of repetitive passages. I apologize to the reader for this inconvenience.

1.3. Statement of co-authorship

Data used in thesis originated from various sources. The electronic tagging data used in chapter 3 and 5 were collected as part of collaborative work between Fisheries and Oceans Canada, the Fish, Food, and Allied Workers, and myself. The conventional tagging data used in chapter 5 originated from three tagging programs, for which proper citation and acknowledgements are provided in the manuscript. Fishery landings data used in chapter 4 were provided by Fisheries and Oceans Canada. The data on nearshore fishes of Bonne Bay presented in chapter 4 were collected by Memorial University undergraduate students and their instructors (Drs. Joe Wroblewski , David Methven and Craig Purchase) as part of a field course taught at the Bonne Bay Marine Station, a course for which I was a teaching assistant during three years. I collected the data on maturity and length at age frequency presented in chapter 4 in collaboration with Bonne Bay local fisherman Keith Reid. I designed the research proposal, performed data analyses (except for the genetic analyses in chapter 4), and wrote the manuscripts included in this thesis.

Chapter 2 is adapted from my doctoral comprehensive examination. I am the single author.

A. Le Bris. Mechanisms of variation in the migratory behaviour of marine fishes with emphasis on Atlantic cod. Manuscript to be submitted to Reviews in Fish Biology and Fisheries.

Chapter 3 and 5 are co-authored with my two co-supervisors, Alain Fréchet and Joe Wroblewski, who made intellectual contributions through development of the project, and through revisions and comments to the initial manuscripts. Chapter 3 is also co-authored with Peter Galbraith, who provided bathymetry and bottom temperature grids for the Gulf of St. Lawrence and made intellectual contributions with his comments to the manuscript.

A. Le Bris, A. Fréchet, P.S. Galbraith, and J.S. Wroblewski. 2013. Evidence for alternative migratory behaviours in the northern Gulf of St. Lawrence population of Atlantic cod (*Gadus morhua* L.). ICES Journal of Marine Science, 70: 793-804.

A. Le Bris, A. Fréchet, J.S. Wroblewski. 2013. Combining electronic tagging and conventional tagging to redesign fishery closed areas. Fisheries Research, 148: 106-116.

Chapter 4 is not intended for publication; however, length frequency data and juvenile abundance analyses have been including in the following manuscript:

A. Le Bris, Currie J., Bruce J.E.B, deYoung B., Methven D.A., Schneider D.C., Wroblewski J.S. Nearshore Fish Fauna of Bonne Bay, a Fjord in Western Newfoundland. In revision.

Genetic analyses presented in chapter 4 were performed by Alexandra Valentin and Jean-Marie Sévigny (Maurice-Lamontagne Institute, Fisheries and Oceans Canada) and are part of the following manuscript:

A.E. Valentin, Sévigny J.-M., **Le Bris A.**, Hooper R.G. Fjords as natural laboratories to address issues of population connectivity in marine species: the contrasting cases of redfish (*Sebastes* sp) and cod (*Gadus morhua*) in the St. Lawrence system (Canada). In revision.

Chapter 2. Mechanisms of Variation in the Migratory Behaviour of Marine Fishes with Emphasis on Atlantic Cod

Abstract

Marine fishes exhibit extensive individual variation in the expression of migratory behaviour. Understanding the mechanisms responsible for the evolution and maintenance of this variation is paramount to predict changes in population distribution in response to ongoing natural and anthropogenic disturbances. This review examines interplays between genetic, environmental, and social factors in shaping the migratory behaviour of marine fish species. Evidence for fine-grained responses to environmental changes suggests that phenotypic plasticity accounts for a substantial part of the variation observed in the migratory behaviour of marine fishes. However, because the genetic basis and the heritability of migratory traits have been overlooked, the relative contributions of genetic, environment, and genetic by environment interactions in the variation of migratory traits have not been quantified in any marine fish species. Similarly, the influence of social transmission in maintaining adaptive and maladaptive variation in migratory behaviours remains speculative. Throughout the chapter, I address methodological issues and highlight how current developments in marine genomics, marine fish tracking technologies, and statistical modeling should help fill these knowledge gaps.

2.1. Introduction

Marine fishes exhibit extensive individual variation in the expression of migratory behaviour. A migratory behaviour can be defined as a set of correlated behavioural traits that involves the cyclic displacement of an individual organism between well-defined and well-separated areas (Harden Jones, 1968; Dingle, 1996). Traits that comprise migratory behaviours include the propensity to migrate, the timing, distance, direction, and patterns of migration. Intrapopulation variation in timing, distance, direction and patterns is termed differential migration and is widespread among marine fish species (Dingle, 1996). Intrapopulation variation in the propensity to migrate is termed partial migration and evidence for its prevalence in marine fish species is increasing (Secor and Kerr, 2009; Chapman et al., 2012b). While individual variation is often considered as noise in fisheries science, it constitutes nevertheless the raw material for adaptive evolution. Understanding the forces driving evolution and maintenance of individual variation in the expression of migratory behaviour is paramount to prediction of future distribution of harvested fish populations. The objective of this study is to review the mechanisms responsible for individual variation in the migratory behaviour of oceanodromous fish species (fish species that migrate within the marine environment).

Migratory behaviours are considered as adaptive responses to spatiotemporal fluctuations in habitats quality and resources distribution. For a variation in a migratory behaviour to be adaptive, it must confer a higher fitness to the individuals expressing the

variation in comparison with other individuals (Dodson, 1997). Trade-offs between costs and benefits of migration determine the fitness of migratory phenotypes. As costs of migration decrease, or conversely benefits of migration increase, the frequency of migrants over non migrants should increase. Benefits of migration that increase fitness include: i) enhanced growth through improved feeding opportunities and decreased inter and intra-specific competition (Brönmark et al., 2008); ii) enhanced survival through avoidance of adverse oceanographic conditions (Fréchet, 1990); and iii) enhanced reproduction through increased mate availability (Domeier and Colin, 1997) and access to spawning grounds that increase offspring growth and survival (Cushing, 1990; Kristiansen et al., 2011). Migration costs that decrease fitness include: i) increased predation due to higher mobility (Werner and Hall, 1988); and ii) reduced energy allocation to growth and reproduction due to energetic demands to carry out migration (Bernatchez and Dodson, 1987), and energy expenditures to develop physiological and morphological traits to perform and regulate migration (Åkesson and Hedenström, 2007; Ramenofsky and Wingfield, 2007).

Evolutionary theory predicts that natural selection of the fittest phenotype erodes variation. To understand the variation observed in the migratory behaviours of marine fishes, we must analyze the genetic and environmental sources of variation, as well as their interactions. Without an underlying genetic basis, a phenotypic trait cannot evolve. The influence of genotypic variation is thus fundamental to the evolution of migratory behaviours. Gene expression is influenced by the environment. The property of a single

genotype to produce different phenotypes in response to changes in environmental conditions is termed phenotypic plasticity (Schlichting and Pigliucci, 1998). The set of behavioural phenotypes that an individual expresses in a specific set of environments is called a behavioural reaction norm (Dingemanse et al., 2010). When direction and amplitude of phenotypic responses to a specific environmental change differ among genetic variants, there is genotype by environment interactions (G×E). It is often the G×E interactions that are critical to understanding the phenotypic patterns observed in nature (Conover and Schultz, 1995).

Historically, tremendous effort has been placed to characterize individual variation and to identify the ecological causes of variation in migratory behaviour (Harden Jones, 1968; Leggett, 1977; Northcote, 1978; Chapman et al., 2012a). The direct (emigration - immigration balance) and indirect (action on life-history) consequences of individual variation in migration on population distribution, dynamics, and resilience (Hilborn et al., 2003; Kerr et al., 2010), on ecosystem trophic dynamics (Schindler et al., 2003; Brodersen et al., 2008a; Brodersen et al., 2011), and on conservation and management measures (Grüss et al., 2011a; Le Bris et al., 2013b) are increasingly well documented. However, the relative contribution of genotype, environment, and G×E interactions in the evolution and maintenance of this variation remains poorly understood in marine fishes, especially in comparison with insects, birds, freshwater fishes, and

diadromous[2] fishes (Hendry et al., 2004; Pulido, 2007; Roff and Fairbairn, 2007; Brönmark et al., 2013). Furthermore, how the social environment acts as a source of variation in marine fish migratory behaviour remains unclear, despite recent calls to acknowledge the role of the cultural inheritance in the evolution of phenotypic variation (Danchin et al., 2011; Day and Bonduriansky, 2011). In the face of current changes in water temperature, ocean acidification, coastal habitat fragmentation, and intense fishing pressure, a better grasp on the genetic control of migration, the capacity for plasticity in migration, and the preponderance of learning and conservatism in migration is needed if we aim to predict changes in distribution and capacity for resilience of marine fish populations.

This review is divided into four parts. The first part introduces the genetic basis of migratory behaviour and underlines the need to measure heritability and genetic correlation of migratory traits in marine fish species. The second part demonstrates that several forms of phenotypic plasticity account for variation in marine fish migratory behaviours, and considers the role of phenotypic plasticity as a promoter or inhibiter of adaptive evolution. The second part also presents the environmental threshold model of migration, a comprehensive model that combines quantitative genetics and a reaction

[2] Diadromous species are species that migrate between the sea and freshwater. Within diadromous species, anadromous species spent most of their adult lives in the sea and migrate to freshwater to spawn, while catadromous species spent most their adult lives in freshwater and migrate to the sea to spawn.

norm approach to explain variation in migration propensity. The third part of the paper reviews evidence of the influence of the social environment as a source of variation in marine fish migratory behaviours. Finally, the fourth part synthesizes the three previous parts using the case study of Atlantic cod (*Gadus morhua*). It is suggested that the environmental threshold model can account for the three sources of variation in the migratory behaviour of Atlantic cod. In each part, I address methodological issues and highlight how current developments in marine genomics, marine fish tracking technologies, and statistical modelling should help fill knowledge gaps. Throughout the paper, anthropogenic factors are considered as part of the environment and no special attention is placed on them, even though topics such as fishery-induced changes in migratory behaviours are of great interest and concern (Quinn et al., 2007; Jørgensen et al., 2008; Thériault et al., 2008).

2.2. Genetic basis of variation in migratory behaviour

Due to the evident influence of adult migration on gene flow, genetic studies of marine fish migration have focused on the consequences of migration on population structure and local adaptation (Conover et al., 2006; Hauser and Carvalho, 2008). Studies on the influence of genetic factors on the migratory behaviours of marine fishes are lacking, as much as studies examining the evolutionary potential of marine fish migratory behaviours. Existence of diverse and specialized behaviours such as natal homing,

homing to spawn, and residency in some marine fish species (Meyer et al., 2000; Robichaud and Rose, 2001; Thorrold et al., 2001), suggest that migratory behaviours may be under genetic determinism and subject to evolutionary change.

2.2.1. Standing genetic variation

Natural selection acts on phenotypic variation regardless of the genetic basis. Evolution, cross-generational changes in gene-frequency, however requires that genetic variation is present in order to proceed. In constant environments, directional and stabilizing selection tend to erode genetic variation through the fixation of genes that influence favoured phenotypes. Genetic drift also has the potential to erode genetic variation in small populations. Three mechanisms are traditionally suggested as sustaining genetic variability in constant environments: the mutation-selection balance, antogonistic pleiotropy, and balancing selection (Cockburn and Hansen, 1991). Directional selection is slow to remove non-adaptive genetic variation perpetuated by random mutations. When numerous loci governed expression of a single trait (*i.e.* polygenic trait), as it is likely the case for migratory traits (Roff and Fairbairn, 2007), per-trait mutation rates can be fairly high because the number of loci potentially subject to mutation is high. In heterogeneous environments, temporal fluctuations help maintaining genetic variation if rates of selective pressure reversal exceed rates of genetic variation depression caused by natural selection.

These mechanisms suggest that, similar to other phenotypic traits such as life-history traits (Stearns, 1992), there is theoretically no shortage of genetic variation for migratory traits. However, it is necessary to demonstrate their genetic basis. A strong means to determine the genetic basis of a phenotypic trait is to use common rearing experiments (also termed common garden experiments), in which individuals from several families or from several populations are reared in controlled environmental conditions. If individuals from distinct families or populations show consistent differences in the expression of a trait under similar environmental conditions, then the trait expression must have a genetic basis. To avoid potential bias induced by maternal effects (although of less concern for fish species that show little parental care), it is preferable to compare offspring of parents that have been reared in similar controlled conditions. Extrapolation of results from common rearing experiments to wild populations can be complicated by genotype by environment interactions. Experiments must thus be conducted across multiple environmental conditions that encompass the range found in nature (Conover et al., 2006). Likely due to these logistic difficulties, few common rearing experiments have been undertaken with marine fish (but see Conover et al., 2006; Hutchings et al., 2007; Purchase et al., 2010 for life history traits). Using common rearing experiments to demonstrate the genetic basis of a migratory trait in marine fishes is further complicated by the need of large experimental facilities to quantify migratory traits (*e.g.* migratory propensity, distance, timing).

2.2.2. Heritability and genetic correlation

For a migratory behaviour to evolve, it must not only have an underlying genetic variation, but a portion of this variation must be heritable. Heritability is the measure of resemblance between parents and offspring. It determines how quick a trait expression can respond to selection. Quantitative genetics provides the tools to estimate the heritable components of the genetic variance in migratory traits. In its narrow sense, heritability (h^2) is defined as the proportion of total phenotypic variance observed in a trait that is due to additive genetic variance ($h^2 = V_A / V_P$), and it varies from zero to one (Falconer et al., 1996). A heritability of zero signifies that all the variance observed in a trait expression is attributable to environmental variance. The effects of selection does not induce change in gene frequency in the offspring population. As heritability tends toward one, the phenotypic variance is increasingly attributable to the additive genetic variance and responses to selection occur more quickly for selective pressures of equivalent strength. It is thought since Fisher's theorem (1930) that the more a trait is related to fitness, the stronger the natural selection acts on it to erode its additive genetic variance, and the less the variance in trait expression remains heritable. Behavioural traits such as traits composing migratory behaviours may be more heritable than life history traits and less heritable than physiological and morphological traits (Mousseau and Roff, 1987).

Migratory behaviours are part of the migratory syndrome, a suite of correlated morphological, biochemical, physiological, and behavioural traits that enable migratory

activity (Dingle, 2006; Dingle and Drake, 2007). Traits that comprise migratory behaviours are thus likely genetically correlated with morphological, biochemical, and physiological traits owing to linkage and pleiotropy. Genetic correlations arise whenever selection simultaneously acts on two or more phenotypic traits (Roff, 1997). As selection on one migratory trait can indirectly drive evolution of other correlated migratory traits, estimations of the sign and magnitude of genetic correlation among migratory traits and with other phenotypic traits are required to predict evolutionary trajectories of migratory behaviours.

2.2.3. Measuring heritability and genetic correlation

Several approaches can be used to partition the additive genetic variance of migratory traits and the additive genetic covariance among migratory traits from other sources of phenotypic (co)variance. Importantly, all approaches require knowledge of the parental relationship between study individuals. Selection and regression experiments (see Falconer et al., 1996), which measure the resemblance between related individuals, have long been used to estimate heritability and genetic correlation in migratory traits, especially in birds (Pulido and Berthold, 2003). A relatively new and increasingly used quantitative genetic approach to estimate heritability and genetic correlations between traits in wild populations is the "animal model" (Kruuk, 2004; Postma and Charmantier, 2007; Kruuk et al., 2008; Wilson et al., 2010). Animal models are mixed-effects models that partition observed phenotypic variance into its genetic and environmental

components. Phenotypic traits measured over an extended period are modeled by treating the breeding value of individual fish as a random effect. Estimation of the variance of the random effect provides an estimate for the additive genetic variance. Multivariate mixed-effects models of several traits allow estimation of genetic correlations among traits. Furthermore, G × E interactions can be assessed by measuring a trait from several individuals across several environments and modeling the trait measured in each environment as distinct traits (Wilson et al., 2010).

Specific to migratory traits, animal models are traditionally applied to mark-recapture data (Charmantier and Gienapp, 2014) but they have not been used with marine fish species. New fish tracking technologies provide the tools to quantify several migratory traits for individual fish over long periods and distances (Block et al., 2001; Le Bris et al., 2013a). Mixed-effects models are increasingly used to consider individual variability in electronic tagging data while modeling migratory traits (Bestley et al., 2009; Peklova et al., 2012). Combining migratory traits and environmental variables measured from electronic tagging experiments with parentage information into the mixed-effects model framework of animal models may help in estimating heritability and genetic correlation of marine fish migratory traits. To obtain the parentage information between tagged individuals is likely the most challenging part in such field studies. Indeed, the lack of parental care, the presence of polygamous mating systems, and the high mobility and dispersal in marine fishes often prevent direct observations of pedigree structure (Wilson and Ferguson, 2002). Molecular pedigree analyses can provide alternatives to

obtain parentage information, especially if the study focuses on cohorts from relatively small-scale populations with known spawning ground, limited eggs and larvae dispersal, and high local recruitments (Wilson and Ferguson, 2002).

Combining electronic tagging experiments with common rearing experiments could be another alternative to quantify heritability and genetic correlation of migratory traits in marine fishes. Fish with known parentage relationships are reared in controlled environments, tagged, and released in nature. Once migratory traits of released individuals are measured from electronic tagging data, heritability and genetic correlation can be estimated using the animal model. Rearing of individuals in control environments provides the necessary parentage information and helps control maternal effects (if studied individuals are offspring of parents reared in common environments) and environmental factors experienced during fish early life. Electronic tagging provides the method to quantify migratory traits for extended periods in natural environments and to measure additional environmental variables of interest.

2.2.4. Evidence of heritability and genetic correlations in migratory traits

To my knowledge, no study has quantified heritability of migratory traits and genetic correlation between migratory traits and other phenotypic traits in marine fish species. Quantitative genetic parameters of migratory behaviour have been estimated in other animal taxa. Kent and Rankin (2001) have demonstrated the presence of a large amount of additive genetic variance in the flight propensity (an index of migration propensity) of

the North American grasshopper (*Melanus sanguinnipes*), with heritability values ranging between 0.50 and 0.60. The amount of migratory activity of the European blackcap (*Sylvia atricapilla*) is heritable (h^2 = 0.37-0.46; Berthold and Pulido, 1994), as is the timing of autumn migration (h^2 = 0.34-045; Pulido et al., 2001). These estimates of heritability suggest that the European blackcap has a potential for rapid adaptive evolutionary changes in migratory traits (within 10-20 generations). A heritability of 0.54 has been estimated for the arrival date of the barn swallow (*Hirundo rustica*) on breeding grounds, and arrival date on breeding grounds is genetically correlated with tail length in males (r_G = 0.275; Moller, 2001). In salmonids species, using a combination of common rearing and mark-recapture experiments, Quinn et al. (2000) showed that timing of return migration in two populations of Chinook salmon (*Oncorhyncus tshawytscha*) from New-Zealand was heritable and highly correlated with the timing of maturation (r_G = 0.92), suggesting that timing of migration can quickly respond to selection (within 30 generations) and can further drive evolution of other phenotypic traits through reproductive isolation. Using molecular pedigree analysis and the animal model, Thériault et al. (2007) showed that the propensity to migrate in a wild population of brook charr (*Salvelinus fontinalis*) is heritable (h^2 = 0.52 - 0.56) and genetically correlated with body size (r_G = -0.52). These examples from various taxa suggest that the migratory behaviour of marine fishes should be heritable and correlated with other phenotypic traits from the migratory syndrome.

2.2.5. Genetic architecture of migratory behaviour

Classical quantitative genetic methods allow useful inferences about inheritance and evolutionary potential of phenotypic traits without explicit identification of the genetic markers involved. Identifying genes that regulate the expression of migratory behaviours can greatly benefit predictions of rates and directions of the evolution of migratory behaviours. Little is known about the genetic architecture of migratory behaviours (Liedvogel et al., 2011). New genomic approaches such as genome scan, candidate gene, and quantitative trait loci are increasingly used to detect markers under selection in marine fishes (Nielsen et al., 2009a). Tests for correlation between differential gene expressions and alternative migratory behaviours are absent in marine fish species, but growing in other animal taxa. A candidate gene approach has recently suggested that the loci ADCYAP1 is involved in the regulation of within and among populations variation in migration propensity in the passerine bird European blackcaps (Mueller et al., 2011). Analyses of differential gene expression in populations of resident and migratory brown trout (*Salmo trutta*) and Atlantic salmon have suggested that 12 genes were involved in pre-adaptations to seawater migration (Giger et al., 2008). Furthermore, a large gene set has been identified in the regulation of timing of migration in Atlantic salmon (Aubin-Horth et al., 2009).

2.3. Plasticity in migratory behaviour

A portion of the total phenotypic variance observed in the migratory behaviour of marine fishes is due to environmental variation. Phenotypic plasticity allows organisms to react to internal or external environmental stimulus by altering form, rate, and direction of phenotypic expression (West-Eberhard, 2003). Phenotypic plasticity concerns virtually all traits (molecular, physiological, morphological, and behavioural) and is a universal property of living organisms (Schlichting and Pigliucci, 1998). Behavioural reaction norms are the linear or non-linear functions used to visualize and quantify changes in the expression of a behavioural trait across an environmental gradient (Figure 2.1a). If the response to an environmental change differs across individuals (or groups of closely related individuals), the reaction norm has a genetic basis and reflects genotype by environment interactions (G × E interactions, Figure 2.1b). Elevation of a behavioural reaction norm describes the mean phenotype ("personality"; Dingemanse et al., 2010), while slope informs on the capacity of an individual to express plasticity. Behavioural reaction norms can be used to measure variation in continuous traits, such as migration timing, distance, and patterns, as well as variation in discrete traits such as migration propensity.

2.3.1. Plasticity in timing, distance, and patterns of migration: dynamic reaction norms

Marine fishes display great plasticity in timing, distance, and patterns of migration. Continuous phenotypic responses to environmental gradients are termed dynamic reaction norms (Sultan and Stearns, 2005). Plasticity in vertical distribution during migration in response to internal (*e.g.* endogenous circadian clock) and external stimulus (*e.g.* light intensity, temperature, food availability) attest for the presence of dynamic reaction norms in the migration patterns of marine fishes (Reebs, 2002). A growing number of studies have demonstrated plastic responses in the migration patterns of pelagic fishes to declining oxygen concentrations in the environment and consequent expansion of oxygen minimum zones (Gilly et al., 2013). For instance, Blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) alter their vertical distribution in order to avoid oxygen minimum zones in the eastern tropical Atlantic (Prince et al., 2010). Chilean jack mackerel (*Trachurus murphyi*) displays plasticity in schooling behaviour during migration in response to prey availability and oxygen concentration (Bertrand et al., 2006). Dynamic reaction norms also characterize plasticity in migration distance and timing. Evidence for changes in marine fish migration distance and timing in response to changing water temperatures is increasing (Perry et al., 2005; Pinsky et al., 2013). For instance, European flounder (*Platichthys flesus*) spring migration hastened during a water cooling event (Sims et al., 2004), and greater amberjack (*Seriola dumerilii*) migration out of the Mediterranean Sea western basin has advanced with increasing water temperature

(Lejeusne et al., 2010). Small short-lived mobile fish species have a high potential for dynamic reaction norms. Capelin (*Mallotus villosus*) in the North Atlantic has undergone large change in migration distance as a result of fluctuating water temperature (Rose, 2005) and population density (Carscadden et al., 2013). Furthermore, a common rearing experiment has demonstrated phenotypic plasticity in capelin usage of spawning sites induced by variation in water temperature (Penton and Davoren, 2013).

Changes in marine fish migratory behaviours are principally inferred from fisheries data and scientific surveys, which demonstrate fine-grained population responses to environmental changes, but do not provide unequivocal evidence of phenotypic plasticity as genetic factors cannot be ruled out (Merilä and Hendry, 2014). In the wild, behavioural reaction norms are best tested using individual responses across multiple years (Dingemanse et al., 2010). Electronic tags, which allow repetitive measurements of individual migratory traits while recording surrounding environmental variables, provide new opportunities to quantify dynamic reaction norms in migratory traits across various environmental gradients. With current improvements in tag memory and battery life, multi-year datasets may soon provide direct evidence of year to year plastic responses matching environmental changes at the individual level. Opportunities for multi-year recording of migratory behaviour should be considered in new electronic tagging programs.

2.3.2. Plasticity in propensity to migrate: obligate and facultative partial migration

Another form of phenotypic plasticity in migration is the capacity of individual fish to adopt either a migratory or a resident tactic (*i.e.* alternative migratory tactics; Dodson et al., 2013). The presence of both tactics within a population is termed partial migration. Empirical evidence suggests that partial migration is a conditional strategy in which environmental conditions experienced during development of an individual drive its propensity to migrate (Jonsson and Jonsson, 1993; Brodersen et al., 2008b; Kerr and Secor, 2010). If the adopted migratory tactic is fixed throughout an organism life-time (*i.e.* obligate partial migration; Chapman et al., 2011), then the reaction norm is imprinted (*i.e.* environmental effects on early life history determine in a definitive way individual phenotype; Sultan and Stearns, 2005). Obligate partial migration is common in salmonidae (Jonsson and Jonsson, 1993). It has been observed in freshwater cyprinidae (Brodersen et al., 2008b) and in estuarine dependent moronidae (Kerr et al., 2009). It may be more prevalent in marine fish species than currently documented (Chapman et al., 2012b). As an instance, a portion of the Mediterranean population of Atlantic Bluefin tuna (*Thunnus thynnus*) exhibits residency within the Mediterranean Sea while another migrates into the Western Atlantic Ocean (Rooker et al., 2008). Obligate partial migration also seems to prevail in a population of spotnape cardinalfish (*Apogon notatus*) from the Uwa Sea in Japan. Some individuals reside year round in coastal breeding areas while

other individuals migrate from coastal breeding areas to deep-water wintering areas (Fukumori et al., 2008).

Comparison of elemental and isotopic signatures of fish organic and biomineralized tissues, especially of the metabolically inert otoliths, with the chemical composition of the water column at pre-determined sites or across spatial gradients offers one solution to infer life-time migratory behaviour of individual marine fishes (Campana, 1999; Hobson, 1999). The relative homogeneity of the main chemical elements in the open ocean and the limited understanding of isotopic variation in marine environments have however impeded detailed reconstructions of marine fish life-time migration patterns from otolith and stable isotope studies (Sturrock et al., 2012; Trueman et al., 2012). Provided that the understanding of the bioincorporation of chemical elements and on the fractionation of isotopes into fish tissues increases, otolith and stable isotope studies offer great promise to test the obligate partial migration hypothesis in marine fish populations.

Partial migration can be facultative: individuals display year to year variation in their propensity to migrate. A special case of facultative partial migration is the skipped spawning partial migration (Shaw and Levin, 2011). This dynamic reaction norm occurs in iteroparous species potentially as a result of trade-offs between current and future reproduction success. Marine fishes tend to skip spawning migration when energetic and mortality costs associated with migration and spawning are high (Jørgensen et al., 2006;

Skjæraasen et al., 2012). Skipped spawning partial migration is thought to be a conditional strategy, in which smaller fish or fish in poor condition favor growth over immediate reproduction in order to increase fecundity in the subsequent years (Engelhard and Heino, 2006; Jørgensen et al., 2006). Stochasticity in environmental conditions tends to increase the frequency of skipped spawning migration (Shaw and Levin, 2011). Skipped spawning partial migration has been documented for several marine fish species, including orange roughy (*Hoplostethus atlanticus*; Bell et al., 1992), Atlantic herring (*Clupea harrengus*; Engelhard and Heino, 2005), Atlantic cod (Jørgensen et al., 2006; Skjæraasen et al., 2012), Pacific halibut (*Hippoglossus stenolepis*; Loher and Seitz, 2008), and may occur in the Western population of Atlantic Bluefin tuna (Block et al., 2001).

2.3.3. The environmental threshold model of migration

The environmental threshold model of migration combines the reaction norm approach and quantitative genetics to understand the evolution and maintenance of alternative migratory tactics in a population (Pulido, 2011). The model assumes that migration propensity is a polygenic threshold trait, "trait with discontinuous emergent phenotypes whose expression is dependent on the liability or switchpoint of an individual relative to some threshold value" (Tomkins and Hazel, 2007). The 'liability' can be seen as a composite trait, which continuous expression is governed by multiple interacting factors, such as individual social status, body size, or growth rate (Roff, 1996; Dodson et al., 2013). In salmonid species, the liability is often expressed in terms of individual body

size (Dodson et al., 2013). An individual adopts a tactic (*e.g.* migration) if its liability value is above the threshold, and the alternative tactic (*e.g.* residency) if its liability value is below the threshold (Figure 2.2). An individual liability is influenced by its genotype and by environmental conditions, and responses to developmental, ecological, or social environments vary among individuals (G × E interactions). Individual liability can be heritable (Páez et al., 2011).

A population mean switchpoint is given by the frequency of individuals adopting one migratory tactic. Populations facing different environments may vary in their average switchpoint (Piché et al., 2008). The frequency of migratory tactics within a population can display short-term changes due to fluctuations in cues distribution, and evolutionary changes due to displacement of switchpoint distribution (Tomkins and Hazel, 2007). Furthermore density-dependent effects can influence the conditional response to internal or external cues, thus affecting tactic frequency in a population (Tomkins and Brown, 2004). An interesting property of the environmental threshold model of migration is that all individuals have the innate ability to migrate (Pulido, 2011). Cryptic genetic variation influencing migration propensity can be suddenly expressed owing to the displacement of the migration threshold, and lead to the reappearance of migratory individuals in resident population, or resident individuals in migratory populations (Pulido and Berthold, 2010). As expected, applications of the environmental threshold model to migratory behaviours have been restricted to animal taxa for which heritability of migratory traits have been documented, such as insects (Roff and Fairbairn, 2007), birds (Pulido et al., 1996; Pulido

and Berthold, 2010), anadromous (Páez et al., 2011; Buoro et al., 2012) and catadromous fishes (Edeline, 2007). To my knowledge, the threshold model has not been applied yet to marine fish species.

2.3.4. Phenotypic plasticity and evolution of migratory behaviour

Paramount to the understanding of variation in marine fish migratory behaviours is the capacity of plastic phenotypic responses to drive genetic evolution. Because environmentally induced phenotypic variations are not directly heritable, phenotypic plasticity was originally thought to shield genotypes from selection, and thus to slow down or hinder evolution. An increasing amount of research argues that selection on recurrent environmentally induced phenotypes can change allelic frequencies (Waddington, 1953; West-Eberhard, 2003; Pigliucci et al., 2006). Another perspective suggests that different types of plasticity facilitate or impede evolution (Price et al., 2003; Ghalambor et al., 2007). To promote evolution, phenotypic plasticity needs to be adaptive and the reaction norm must be heritable.

Phenotypic plasticity can be adaptive, maladaptive or neutral, if the reaction norm increases, decreases, or does not affect individual fitness in the new environment, respectively (Figure 2.1b). Ghalambor et al. (2007) distinguished two types of adaptive plasticity with different consequences for evolution. Adaptive plasticity is perfect when a plastic reaction norm for a trait is optimal (*i.e.* the trait value in the new environment is at the optimum level favored by selection). In this case, the reaction norm does not evolve

and is subject to stabilizing selection. When a reaction norm tends towards the optimum value but does not reach it, adaptive plasticity is incomplete, and the reaction norm gradually evolves under directional selection on extreme phenotypes (Ghalambor et al., 2007). Influence of plasticity on evolution depends on the recurrence of a reaction norm. A continuously variable reaction norm producing a wide range of trait expression is less subject to selection; plasticity is expected to retard evolution (West-Eberhard, 2003). In the case of condition-sensitive switches producing the recurrent expression of an alternative adaptive phenotype, plasticity may accelerate evolution of the favored phenotype (West-Eberhard, 2003). With respect to migratory behaviours, current selection for phenotypic plasticity towards lower migratory activity has been recently suggested to promote evolution of residency in a population of blackcaps (Pulido and Berthold, 2010).

A critical and debated assumption in the hypothesis that adaptive phenotypic plasticity promotes the evolution of phenotypes is that environmentally-induced recurrent phenotypic variations are genetically "assimilated" or "accommodated" (West-Eberhard, 2003; De Jong, 2005; Pigliucci et al., 2006; Crispo, 2007). Genetic assimilation (Waddington, 1953) occurs when stabilizing selection acting on development favors the phenotypes that display adaptive reaction norms. Over time, natural selection acting on environmentally-induced novel phenotypes lead to changes in allelic frequencies, and the environmental signal is progressively no longer required for the phenotypic expression. A similar concept is the Baldwin effect (Baldwin, 1896), which suggests that selection acts

upon standing genetic variation and that evolution proceeds in the direction of adaptive reaction norms. The Baldwin effect implies that the capacity for phenotypic plasticity is directly under the action of natural selection and may increase over evolutionary time (Figure 2.3). In contrast, genetic assimilation leads to canalization of reaction norms (*i.e.* the capacity for phenotypic plasticity is progressively lost, Figure 2.3). Canalization of reaction norms may arise from costs of phenotypic plasticity, such as energetic investment to maintain sensory and regulatory mechanisms and the risk associated with gathering information about the environment (DeWitt et al., 1998; Pigliucci et al., 2006). More recently, the less restrictive term "genetic accommodation" has been proposed to consider novel traits arising from both genetic mutation and environmental induction, as well as the capacity of phenotypic plasticity to increase and decrease over time (West-Eberhard, 2003). Concerns about the genetic assimilation and accommodation concepts have been raised due to the lack of convincing evidence (De Jong, 2005). This underlines the need for more empirical studies to test for the Baldwin effect, genetic assimilation and accommodation, and to determine which process predominates in nature. Nussey et al. (2005) showed that both elevation and slope of the reaction norm of the female great tit (*Parus major*) for egg laying date across a temperature gradient were heritable, suggestive of a Baldwin effect. In contrast, McCairns and Bernatchez (2010) indicated a loss of plasticity in threespine stickleback (*Gasterosteus aculeatus*) in the survival response to change in salinity conditions, suggestive of a genetic assimilation. Both

Baldwin effect and genetic assimilation may occur in nature on different traits (Crispo, 2007).

2.4. Learning of migratory behaviour

2.4.1. Social transmission of migratory behaviour

Apart from genetic and environmental factors, social factors (*i.e.* social transmission from older experienced individuals to younger naïve individuals) may also maintain intrapopulation variation in the migratory behaviour of marine fishes over evolutionary time. Experimental studies have revealed that fish can learn migratory behaviours from conspecifics (Helfman and Schultz, 1984; Laland and Williams, 1997), including maladaptive migratory behaviours (Laland and Williams, 1998). Social transmission of migratory behaviours is facilitated by iteroparity, age structure overlap, and shoaling tendency (Dodson, 1988; Brown and Laland, 2003; Brown and Laland, 2011), three characteristics displayed by numerous marine fish species. The adopted-migrant hypothesis suggests that new spawning migration routes in a population of Atlantic herring (*i.e.* timing, distance, direction) arise from dispersal in unstable populations (*i.e.* following collapse or recruitment boom), and that social transmission from experienced mature fish to naïve immature fish ensures the maintenance of migration routes (McQuinn, 1997). It further suggests that recruiting juveniles adopt the migratory

behaviours of the adult schools that allow for a synchronization of their maturation cycle. Individuals from the same cohort may thus recruit to different adult schools as a result of genetically and environmentally induced variation in development.

Support for the adopted-migrant hypothesis was provided by Corten (2001), who suggested that new feeding, wintering and spawning migratory routes and areas arise accidentally due to dispersal of spawning products when a recruiting year-class lacks guidance from older conspecifics. Huse et al. (2002; 2010) further suggested that establishment of new wintering areas in Atlantic herring is a stochastic process, which results from the disruption of the social transmission mechanism due to a high ratio of naïve / experienced individuals. Experimental and modeling work on decision making in animal group migration has recently demonstrated that a minority of experienced and intransigent individuals can dictate the migratory behaviour of a fish school, but that the growing presence of uninformed individuals can spontaneously reverse the school control to the majority (Couzin et al., 2011). The proportion of experienced individuals over naïve individuals in a fish population may thus contribute to the evolution and maintenance of variation in the migratory behaviour of schooling marine fish species, including maladaptive variation. In schooling fish species, the fact that the behaviour of an individual is constrained by the behaviour of other individuals can impede fitness maximization. Social transmission of maladaptive novelties has been suggested as responsible for the maintenance of costly migration routes in Atlantic herring (Huse et al., 2010).

2.4.2. Learning and evolution of migratory behaviours

Learning allows rapid acquisition of advantageous migratory behaviours (Dodson, 1988). But can learned behaviours lead to evolution of migratory traits? The traditional view of evolution states that because learning is a non-genetic mechanism, it is not subject to evolution. The cultural inheritance hypothesis however suggests that a portion of phenotypic variation is socially inherited (Danchin et al., 2011). Danchin et al. (2004) proposed to include a cultural transmission component in the measure of heritability, such that $h^2 = (V_A + V_{AC}) / V_P$; where V_{AC} is the additive cultural variance. Like other regulatory mechanisms, learning influences frequency and condition of trait expression and may thus theoretically facilitate or impede genetic evolution (note that learning can be considered as a form of plasticity, West-Eberhard, 2003). As an instance, recurrent expression of learned long-distance migration can make visible to selection individual predisposition for long-distance migration (*e.g.* individuals with more streamlined body or higher energy storage capacity; Fraser and Bernatchez, 2005; Åkesson and Hedenström, 2007). If long-distance migration increases fitness, recurrent trait expression caused by learning may enable spreading and fixation (*i.e.* genetic assimilation or Baldwin effect) of the alleles responsible for the development of the traits that facilitate long-distance migration. The learning capacity of an individual may also be selected. The spatial learning hypothesis suggests that individual fish recognize migration routes as a sequence of environmental stimuli (Dodson, 1988). Ability of an individual to adequately identify and respond to stimuli may be subject to selection and be progressively fixed in

the population. In fact the Baldwin effect originally considered individual ability to learn as being subject to evolutionary change (Baldwin, 1896).

2.5. Atlantic cod as a case study

Atlantic cod is an ideal species to synthesize current knowledge on the influence of genetic, environmental, and social factors in the variation of migratory behaviours in marine fishes. Due to its historical, cultural, and commercial importance, Atlantic cod is one of the most intensively studied marine fish species. It exhibits an astonishing variation in migratory behaviour within and among populations (Robichaud and Rose, 2004). Variation is observable in the propensity to migrate, and in the timing, distance, direction, and patterns of migration of Atlantic cod. Some populations migrate hundreds of kilometres between overwintering, spawning, and feeding habitats, while others display life-long residency within a single fjord.

2.5.1. Genetic determinism in cod migratory behaviour

Similar to other marine fish species, direct evidence for genetic determinism and adaptive evolution in Atlantic cod migratory behaviour is lacking. However, several points might indicate that the migratory behaviour of Atlantic cod is partially determined by genetic factors. First, Atlantic cod exhibit several specialized migratory behaviours including, site-fidelity (Wright et al., 2006a), homing to spawn (Robichaud and Rose, 2001), and

natal homing (Svedäng et al., 2007), which limit gene flow across populations, and thus promote genetic isolation. Second, common rearing experiments have demonstrated local adaptation in life-history traits at regional geographic scales (Marcil et al., 2006; Hutchings et al., 2007), which highlight the evolutionary potential in the species. Particularly interesting is a recent common rearing experiment that has demonstrated heritability in Atlantic cod spawning time along the Norwegian coast (Otterå et al., 2012). Because spawning time is often correlated with timing of migration (Quinn et al., 2000; Charmantier and Gienapp, 2014), timing of migration in Atlantic cod may also be heritable. Third, new genomics approaches increasingly reveal correlation between clines in allelic frequency and selective environmental forces, suggestive of within species adaptive divergence at various geographical scales (Nielsen et al., 2009b).

An interesting case is the *Pan* I locus. Consistent differences in allelic frequencies at the *Pan* I locus occur between migratory and resident Atlantic cod in Norway (*i.e.* Northeast-Arctic and Norwegian coastal cod; Sarvas and Fevolden, 2005) and in Iceland (*i.e.* frontal and coastal Icelandic cod; Pampoulie et al., 2008). Individuals migrating from offshore to inshore waters predominantly possess the *Pan* I^{BB} genotype, while inshore resident cod predominantly possess the *Pan* I^{AA} genotype. *Pan* I locus codes for a membrane protein (Pantophysin) expressed in cytoplasmic transport vesicles, but its exact physiological function and the drivers of selection are poorly understood (Pogson and Mesa, 2004). It remains therefore unclear whether this correlation between clines in allelic frequencies and migration propensity reveals the influence of the *Pan* I locus on

cod migratory propensity (potentially via an influence on individual growth rate; Jónsdóttir et al., 2008), or if the observed variation in allelic frequency is a consequence of the divergence in habitat selection (depth, salinity, temperature) between migratory groups, or if it simply reflects non-evolutionary mechanisms (Gould and Lewontin, 1979).

2.5.2. Phenotypic plasticity in cod migratory behaviour

Environmental sources of variation in Atlantic cod migratory behaviour have long been recognized. For instance, Atlantic cod from the Gulf of St. Lawrence has been shown to respond to a water cooling event by migrating earlier, and by increasing distance and depth of the overwintering migration (Castonguay et al., 1999). Cod distance and direction of migration also display plastic responses to changes in population density (Tamdrari et al., 2010). Furthermore, within population plasticity in migration distance and timing has been shown to be influenced by variation in individual length and condition (Jørgensen et al., 2008).

Plasticity is evident in Atlantic cod propensity to migrate. Alternative migratory tactics at spatial scales smaller than scales of observed genetic differentiation appear to prevail in several populations of Atlantic cod, including cod from the northern Gulf of St. Lawrence (Le Bris et al., 2013a), from the east coast of Newfoundland (Wroblewski et al., 1994; Rose et al., 2011), and from the Gulf of Maine (Sherwood and Grabowski, 2010). Furthermore, year to year variation in cod migration propensity can be induced by

skipped spawning. In the Northeast Artic Cod population, skipped spawning partial migration prevails predominantly in females with lower energetic reserves and in smaller and younger adult fish (Skjæraasen et al., 2012). Due to the relatively high energetic costs required to perform vitellogenesis and spawning migration, skipping spawning migration when energetic reserves are low may limit post-spawning mortality. Skipped spawning partial migration may thus reflect a conditional strategy, in which cod perform or not annual migration so as to maximize lifetime reproductive success (Jørgensen et al., 2006). All these observations of rapid changes in cod migratory behaviours (timing, distance, direction, and propensity) suggest that non-genetic sources of variation account for a substantial portion of the observed variation in Atlantic cod migratory behaviours.

2.5.3. Social transmission of migratory behaviour in Atlantic cod

Learning of migratory routes is one hypothesis proposed to explain maintenance of variation in migratory behaviours in Atlantic cod, including the ability to return to a specific site (Harden Jones, 1968). Acoustic surveys of migrating shoals of Atlantic cod have revealed that Atlantic cod migrate in size-structured aggregations, which has led to the speculation that migratory routes are socially transmitted in Atlantic cod (Rose, 1993). Furthermore, tagging studies have demonstrated non-random group cohesion in Atlantic cod (Tamdrari et al., 2012a), and the ability to return to previously used areas after relatively short distance transplantation (Green and Wroblewski, 2000; Robichaud and Rose, 2002). Finally, social factors have been suggested to affect timing of cod migration.

Increased abundance of older cod in the southern Gulf of St. Lawrence population coincided with an earlier departure time for the autumn migration (Comeau et al., 2002a). All these studies suggest that social factors may contribute to the maintenance of variation in the migratory behaviour of Atlantic cod. However, because demonstrating social transmission of migratory behaviour in the wild is challenging, conclusive evidence is still lacking. Furthermore, it remains unclear if social factors (*e.g.* disruption of ratio naïve / experienced individuals) can induce evolution of new migratory behaviours.

2.5.4. Application of the environmental threshold model of migration to Atlantic cod

I previously described how genetic, environmental, and social factors might contribute to the evolution and maintenance of individual variation in the expression of migratory behaviour in Atlantic cod. In this last part, I describe how the environmental threshold model (ETM) of migration can theoretically account for the influence of these three sources of variation on Atlantic cod migratory behaviour.

Assuming that migration propensity is a polygenic threshold trait, the ETM predicts that opposite directional selective pressures in two environments lead to the establishment of two populations with alternative migratory tactics (one resident and one migratory population). Within each environment, stabilizing selection can induce canalization of the average switchpoint of each population (Pulido, 2011). The resident population would display a high average migration switchpoint, while the migratory

population would display a low average migration switchpoint (Figure 2.4). Typically, populations of Atlantic cod that remain resident in inshore waters, such as in Gilbert Bay, Labrador (Green and Wroblewski, 2000), in Trinity Bay, Newfoundland, (Wroblewski et al., 1994), or in fjords along the Norwegian coast (Jakobsen, 1987), would have lower average migration switchpoints. Adjacent migratory populations, such as the northern cod population and the Northeast Arctic cod population would have higher average migration switchpoints. Furthermore, because abundance is traditionally higher in cod migratory populations (Robichaud and Rose, 2004), the frequency distribution of switchpoints should be wider in the migratory population than in the resident population (Figure 2.4).

In the migratory population, several environmentally induced mechanisms may change phenotypic frequencies. First, an increase in costs associated with spawning migration, or a decrease in the condition of maturing cod during a year might displace the migration threshold to the right (Figure 2.4) and increase the proportion of cod skipping spawning migration (Jørgensen et al., 2006; Skjæraasen et al., 2012). Similarly, environmentally induced decline in early life growth rate or in individual body size, might shift the migration threshold to the right, and lead to the adoption of a resident behaviour by some individuals from the migratory population. Naturally, the likelihood of an individual to change migratory behaviour depends upon its sensitivity to environmental condition and to the position of his swichpoint relative to the threshold value.

In the resident population, the cryptic genetic variation regulating expression of migration propensity can be suddenly expressed as a result of environmentally induced (*e.g.* increase in population density) displacement in the threshold value (Pulido, 2011). As the frequency distribution of switchpoints in resident populations is narrower, a significant portion of the population would suddenly migrate (Figure 2.4). That proportion could be further increased by the entrainment of resident individuals by newly migratory individuals (Petitgas et al., 2010). We can speculate that a displacement of the migration threshold resulting from large increase in population density is the mechanism responsible for the observed sudden reappearance of migration in the Smith Sound cod aggregation in Newfoundland (Rose et al., 2011).

2.6. Conclusion

In this chapter I reviewed evidence of the influence of genetic, environmental, and social factors in the evolution and maintenance of individual variation in the expression of migratory behaviour in marine fish species. Individual and population fine-grained responses to developmental and environmental changes suggest that phenotypic plasticity is a main source of variation in the migratory behaviour of marine fishes. Whether this plasticity has some genetic basis (G×E interactions) and can lead to the evolution of migratory behaviours remains to be demonstrated. Furthermore, there is a need to estimate quantitative genetic parameters (heritability and genetic correlation) of migratory

traits in order to predict rates and directions of the evolution of migratory behaviours. Whether the lack of quantitative genetic study on marine fish migration reflects the difficulties to quantify migratory traits of marine fishes, the logistical challenges associated with common rearing experiments, or the common beliefs in fisheries science that adaptive genetic changes occur only at time scales irrelevant to fisheries management (Carvalho, 1993; Conover and Munch, 2002; Conover et al., 2005), new experimental protocols are needed. Recent advances in fish tracking technologies, fish farming, marine genomics, and statistical ecology offer great prospects in that regard. Combining the electronic tagging of small cohorts with common rearing experiments or pedigree analyses, appears as one promising solution to quantify the effects of genotype, environment, and genotype by environment interactions on the individual variation observed in the migratory behaviour of marine fish species.

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Figures

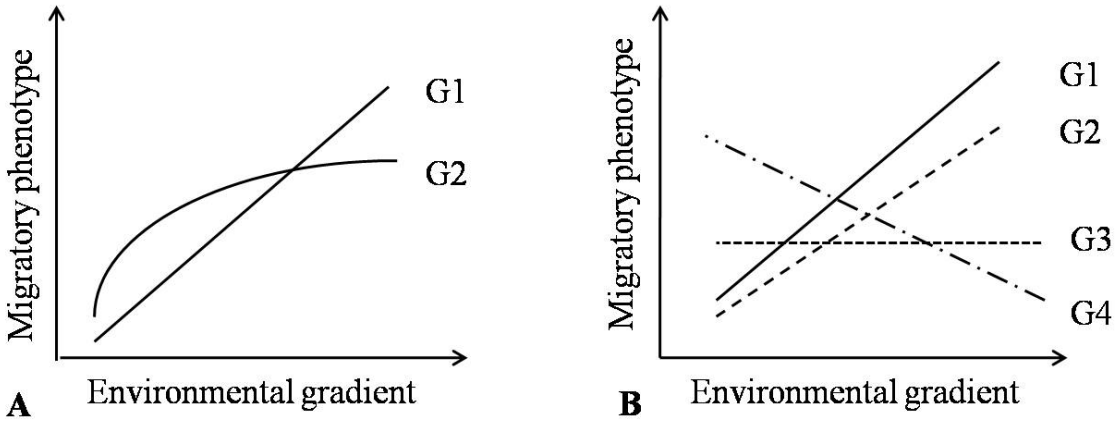

Figure 2.1. A) Hypothetical migration reaction norms for 2 genotypes across an environmental gradient. Genotype 1 has a linear reaction norm. Genotype 2 has a non-linear reaction norm. B) Hypothetical migration reaction norms for 4 genotypes across an environmental gradient. The highest phenotypic value is assumed to have the highest fitness. Genotype 3 shows a neutral (flat) reaction norm. The reaction norm of genotypes 1 and 2 increase their fitness. Genotype 1 displays a more plastic reaction norm than genotype 2 (higher slope). The reaction norm of genotype 4 decrease its fitness.

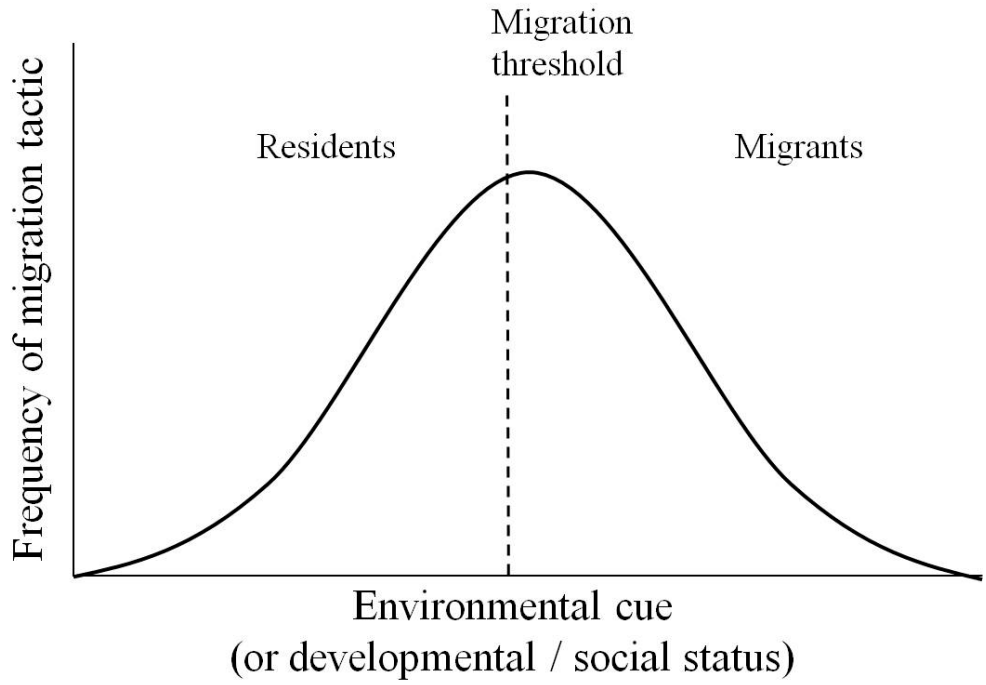

Figure 2.2. The environmental threshold model of migration (adapted from Pulido, 2011). The propensity of an individual to migrate is determined by the position of its switchpoint with respect to a threshold level (dotted vertical line). Fish with a switchpoint below the threshold level adopts a resident phenotype. Fish with a switchpoint above the threshold level adopts a migratory phenotype. A shift to the right of the environmental threshold increases the proportion of resident fish in the population. A shift to the left increases the proportion of migratory fish in the population.

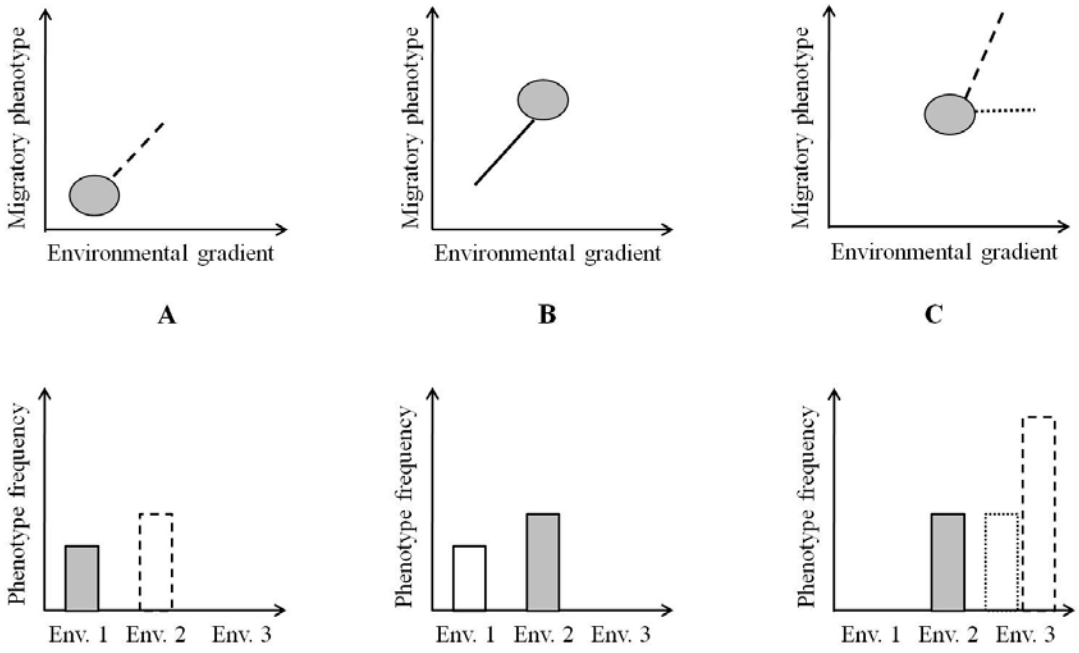

Figure 2.3. Genetic assimilation and Baldwin effect for continuous (top panels) and discrete (bottom panels) migratory traits (adapted from Pigliucci et al., 2006 and Crispo, 2007). Grey circles show realized mean population phenotype (*e.g.* wintering migration distance). Dashed and dotted lines show pre-existing potential for plasticity. Grey stacks show the frequency of a discrete phenotype in a fish population (*e.g.* frequency of migrants). Dashed and dotted stacks show pre-existing potential for plasticity. A) The population displays potential for plasticity, should the environment change. B) Population reaction norm reveals an increase in the mean phenotypic value and in the frequency of the discrete phenotype. C) Selection keeps operating in the new environment and induces genetic fixation of the new phenotype. If the genetic fixation corresponds to a genetic assimilation, stabilizing selection induces loss of the capacity for plasticity, should the environment changes again (dotted line and stack). If the genetic fixation corresponds to a Baldwin effect, differential selection can increase the capacity for plasticity, should the environment changes again (dashed line and stack).

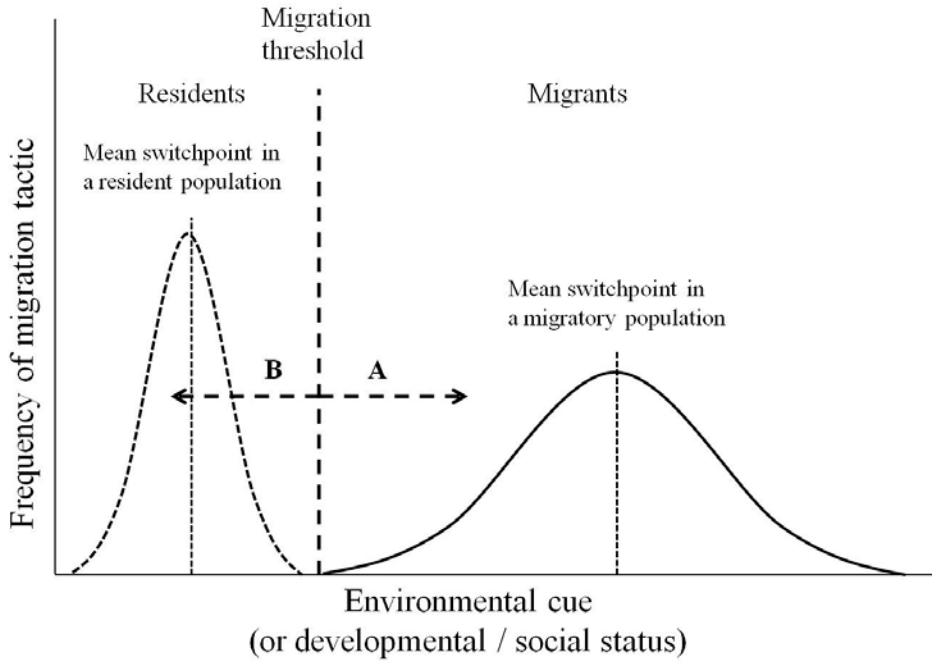

Figure 2.4. Environmental threshold model of migration for a resident (dashed curve) and a migratory population (solid curve) of Atlantic cod. A) Changes in one or several environmental gradients progressively displace the migration threshold to the right. As the frequency distribution of switchpoint is relatively wide in the migratory population, a small portion of the population progressively adopts a resident tactic. B) Changes in one or several environmental gradients progressively displace the migration threshold to the left. As the frequency distribution of switchpoint is relatively narrow in the resident population, a large portion of the population suddenly adopts a migratory tactic.

Chapter 3. Evidence for Alternative Migratory Behaviours in the Northern Gulf of St. Lawrence Population of Atlantic Cod

Arnault Le Bris[1*], Alain Fréchet[2], Peter S. Galbraith[2], Joseph S. Wroblewski[3]

[1]Biology Department, Memorial University of Newfoundland, St. John's, NL, Canada

[2]Maurice-Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC, Canada

[3]Department of Ocean Sciences, Memorial University of Newfoundland, NL, Canada

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Abstract

Individual variation in migration propensity affects population dynamics and connectivity. The diversity of migratory behaviours of Atlantic cod (fork length >40 cm) in the northern Gulf of St Lawrence was studied using data-storage tags that record depth and temperature. Movement patterns of Atlantic cod equipped with data-storage tags were reconstructed using a geolocation model based on daily maximum depth and bottom temperature. Reconstructed migration routes revealed the previously undocumented coexistence of resident and migratory individuals in the population. Migratory cod overwintered in relatively deep (300–500 m) and warm (5°C) waters, while residents displayed a prolonged period of immobility in shallow (<100 m) and near-freezing (–1.5°C) coastal waters of western Newfoundland. In the spring, migratory cod displayed extensive diel vertical migration suggestive of spawning behaviour. The presence of alternative migratory behaviours should be considered in the spatiotemporal management of the collapsed population.

3.1. Introduction

Individual variation in migration propensity affects fish population structure, productivity, stability, and resilience (Kerr et al., 2010), and induces top-down effects on ecosystem trophic dynamics (Brodersen et al., 2008a). Indeed, variation in the proportion

of fish remaining within an area affects the community structure and population abundance at lower trophic levels upon which they feed (Post et al., 2008; Brodersen et al., 2011). At the two endpoints of a behavioural gradient are found resident and migratory individuals (Cagnacci et al., 2011). Alternative migratory tactics (residency and migration) may reflect behavioural differences at the population level between genetically distinct and locally adapted populations. Alternative migratory tactics may also reflect within-population behavioural differences that arise from a conditional strategy, in which the tactic adopted by an individual depends upon a genetically determined threshold level for specific environmental, developmental, and/or social cues (Chapman et al., 2011; Pulido, 2011). The coexistence of resident and migratory individuals within a population is termed partial migration and appears to prevail in plenty of anadromous and marine fish species (Jonsson and Jonsson, 1993; Chapman et al., 2012b).

Throughout its geographic range, Atlantic cod (*Gadus morhua*) display diverse migratory behaviours (Robichaud and Rose, 2004). The flourishing of fish tracking technologies has helped recognize that numerous putative populations of Atlantic cod comprise a mixture of resident and migratory individuals (Green and Wroblewski, 2000; Neat et al., 2006; Svedäng et al., 2007). Metapopulation theory and partial migration theory have thus gained attention to explain variability in cod migratory behaviour and its consequences on population structure (Smedbol and Wroblewski, 2002; Wright et al., 2006b; Petitgas et al., 2010; Sherwood and Grabowski, 2010). While metapopulation structure implies spawning isolation with some degree of connectivity between

subpopulations, partial migration focuses on the individual variability in migration propensity within a panmictic population.

Atlantic cod show inter and intrapopulation variability in the propensity to migrate not only horizontally but also vertically (Righton et al., 2001; Neat et al., 2006). Periodicities in the vertical movement of cod may reveal periods of foraging, resting, and spawning (Stensholt, 2001). Linking horizontal and vertical movement patterns, and thermal conditions experienced during migration, may help understanding of the behavioural dynamics of alternative migratory tactics within population of Atlantic cod (Pálsson and Thorsteinsson, 2003; Hobson et al., 2009).

The Atlantic cod population from the northern Gulf of St. Lawrence (nGSL) [Northwest Atlantic Fisheries Organization (NAFO) divisions, 3Pn, 4RS] is managed as a single population. General patterns of migration documented with traditional tagging studies have revealed distinct seasonal habitats (Templeman, 1979; Yvelin et al., 2005). Atlantic cod overwinter outside the Gulf on the northern slope of the Laurentian Channel (Campana et al., 1999; Castonguay et al., 1999), migrate in spring to start spawning near St George's Bay (Ouellet et al., 1997; Méthot et al., 2005), and reach summer coastal feeding areas located along the west coast of Newfoundland, the Strait of Belle Isle, and the Québec North Shore (Figure 3.1). Contrasting with numerous populations of Atlantic cod from Eastern Newfoundland (Wroblewski et al., 1994), Labrador (Green and Wroblewski, 2000), and Norway (Espeland et al., 2008), no resident behaviour has been

documented in the northern Gulf of St Lawrence (nGSL) population, reflecting the knowledge gap on the diversity of migratory behaviours in the population.

The main objective of the study was to characterize the diversity of migratory behaviours in the nGSL Atlantic cod population using data-storage tags (DSTs). Specifically, we tested the hypothesis that the population comprises a mixture of resident and migratory individuals. To test this hypothesis, movement patterns of cod equipped with DSTs were reconstructed using a geolocation model based on daily maximum depth and associated temperature. Periodicities were sought in the vertical movement of Atlantic cod in order to characterize the behavioural dynamics of each hypothesized migratory tactic.

3.2. Material and Methods

3.2.1. Tagging procedure

In 2007, the Department of Fisheries and Oceans (DFO) Canada, and the Fish Food and Allied Workers (FFAW) began a tagging program for Atlantic cod in the nGSL using DSTs. Cod were captured using baited handlines at multiple locations along the west coast of Newfoundland and the Quebec North Shore (Figure 3.1). Tagging locations were chosen to encompass the three NAFO management units in the nGSL (NAFO divisions 3Pn, 4R, and 4S). Cod presenting no sign of barotrauma were surgically implanted with

DSTs inside their abdominal cavity. One traditional spaghetti tag with a unique serial number and one red tag labelled with a warning message were fixed in the dorsal musculature of cod in order to inform fishers about the presence of the internal electronic tag. Fish were released immediately after tagging such that the overall procedure seldom took more than two minutes. Advertisement and reward campaigns (100 CAD for each DST) were used to increase the tag-reporting rate. A total of 353 cod (fork length >40 cm) were tagged with DSTs. 14 cod were tagged in 3Pn NAFO management division, 84 in the southern part of division 4R, 149 in the center of division 4R, 38 in the north of division 4R, and 68 in division 4S. As the tagging program progressed, tag series LTD_1100, LAT_1400, and LAT_1500 (Lotek Wireless Inc., St John's, Canada, www.lotek.com) were used. DSTs recorded ambient temperature (±0.2°C accuracy and 0.05°C resolution) and pressure (±1% accuracy and 0.05% resolution). DSTs were programmed using the time extension recording feature in order to privilege sampling duration over frequency. As a result, sampling duration and frequency varied among tags from 54 to 746 days and from 2.5 to 60 minutes, respectively (Table 3.1).

3.2.2. Bottom temperature

The Gulf of St Lawrence is a semi-enclosed sea characterized by a low tidal range and the presence of a unique amphidromic point (point of zero amplitude for one tidal constituent) for the M2 constituent (Saucier et al., 2003). The tidal location method could not be used in this study to estimate fish position (Metcalfe and Arnold, 1997; Hunter et

al., 2003a). Instead, the geolocation method focused on the Gulf complex bathymetry, induced by the presence of three channels (Laurentian, Esquiman, and Anticosti Channels), on the relatively pronounced spatial gradients in temperature, and on the temporal persistence in these temperature gradients (Figures 3.1 and 3.2).

Bottom temperature grids were obtained using all available CTD (conductivity, temperature, and depth) casts sampled by Fisheries and Oceans Canada (typically 250 or more casts per seasons). Temperature profiles were averaged into depth intervals of 1 m and interpolated onto a 2-km resolution grid using the Barnes algorithm (Galbraith, 2006). Minimum and maximum temperatures measured in each of the Gulf's nine oceanographic subareas were used to bind horizontal interpolation of temperature (Tamdrari et al., 2012b). The bottom temperature at each grid-point was obtained by selecting the interpolated temperature at the depth level corresponding to a bathymetry grid obtained from the Canadian Hydrographic Service. Bottom temperature grids were obtained annually for the months of March, June, August, and November from 2007 to 2011. Few stations deeper than 200 metres were sampled in March, inducing gaps in the bottom temperature grid. Deep water temperature is relatively constant throughout the year (Galbraith et al., 2012), thus, gaps were filled using June bottom temperatures. March bottom temperatures were used for the winter, June bottom temperatures for the spring, August bottom temperatures for the summer, and November bottom temperatures for the fall (Figure 3.2).

3.2.3. Geolocation model

A hidden Markov model was used to compute the posterior probability distribution of daily locations of tagged fish (Pedersen et al., 2008; Thygesen et al., 2009). As with other state-space models, hidden Markov models consist of two coupled stochastic models: the process model and the observation model (Cappé et al., 2005). The process model simulates the fish movement in a two-dimensional space. The observation model refines positions predicted by the movement model by comparing data recorded by the tag with data from the bathymetry and bottom temperature grid. This duality allows modelling of errors from the fish movement and from the observation process separately. Hidden Markov models are therefore well adapted to model animal telemetry data (Franke et al., 2004; Patterson et al., 2008).

Assuming that fish movement follows a two-dimensional random walk**,** the time-evolving probability density of fish location can be computed using the diffusion equation (Okubo, 1980; Sibert et al., 2003; Pedersen et al., 2008):

$$\frac{\partial \varphi(\boldsymbol{x},t)}{\partial t} = D\left[\frac{\partial^2 \varphi(\boldsymbol{x},t)}{\partial x_1^2} + \frac{\partial^2 \varphi(\boldsymbol{x},t)}{\partial x_2^2}\right] \qquad (3.1)$$

where $\varphi(\boldsymbol{x}, t)$ is the probability density function of the fish position (*i.e.* the probability that the fish is located at position $\boldsymbol{x} = [x_1, x_2]$ at time *t*), and *D* represents the diffusion coefficient. The diffusion equation was discretized in space (331 × 476 regular grid cells) and time (number of recording days), and was solved using finite differences.

Daily locations predicted by the movement model were refined using an observational likelihood. The observational likelihood consists of assigning, for each time-step, a likelihood value to each grid cell based on the depth and temperature data from the grid and from the tag (Andersen et al., 2007; Pedersen et al., 2008). Under the assumption that cod in the Gulf of St Lawrence visit the seafloor at least once a day, a fairly reasonable assumptions for a demersal species such as cod (Righton and Mills, 2008; Hobson et al., 2009), the daily maximum depth recorded by the tag was considered representative of the sea floor, and the temperature associated with daily maximum depth was considered representative of the bottom temperature. The observational likelihood (*i.e.* likelihood of observations $\boldsymbol{y}$ given position $\boldsymbol{x}$) was computed as the product of two normal cumulative distribution functions assuming that depth and temperature are independent:

$$P(\boldsymbol{y}|\boldsymbol{x}) = \Phi\,(\mu_z, \sigma_z, [z1\ z2]) \times \Phi\,(\mu_{tp}, \sigma_{tp}, [tp1\ tp2]) \qquad (3.2)$$

where $\boldsymbol{y} = [z, tp]$ is the daily maximal depth (z) and temperature (tp) recorded from the tag, [*z1 z2*] is the depth interval defined by the daily maximum depth recorded by the tag and the ±1% accuracy of the pressure sensor, [*tp1 tp2*] is the temperature interval defined by the daily temperature recorded by the tag and the ±0.2°C accuracy of the temperature sensor, μ_z is the grid cell bathymetry, μ_{tp} is the grid cell bottom temperature, σ_z is the standard deviation of the grid cell bathymetry, and σ_{tp} is the standard deviation of the grid cell bottom temperature. In cases when the recapture day corresponded to the last

sampling day, the observational likelihood was implemented with the recapture position reported by fishers and an uncertainty delimited by a 10-km radius circle. A 10-km radius circle was considered appropriate for the recapture location uncertainty since the fishery is now a coastal fishery conducted exclusively with fixed gears.

The diffusion parameter *D* was estimated by minimizing the negative log likelihood function using Matlab R2012a optimization toolbox (The Mathworks, Natick, MA). The last step of the geolocation model consisted of a smoothing filter that refined location estimation by computing the full posterior distribution conditional on all observations (detailed descriptions of the maximum likelihood estimator and of the smoothing filter are provided in Thygesen et al., 2009).

3.2.4. Classification and characterization of migratory behaviour

Migratory behaviours were determined from visual inspection of reconstructed individual spatial distribution. Individual spatial distribution for the period *t* were computed for each cod as the normalized cumulative distribution of daily locations (Pedersen et al., 2011):

$$SD = \frac{1}{\mathrm{t}} \sum_t \varphi(\boldsymbol{x}, t) \qquad (3.3)$$

Cod were visually classified as migrant when they displayed a clear shift in their geographic distribution between two areas of temporal stability regardless of the Euclidian distance (Dingle, 1996; Cagnacci et al., 2011). Cod were otherwise classified as

resident. Once behaviour type was determined, a index for the vertical swimming activity was calculated for each individual following Stensholt (2001):

$$Act(t) = -1 + (maxz + 10) \times (minz + 10)^{-1} \quad (3.4)$$

where *maxz* and *minz* correspond to daily maximum and minimum depth respectively. The vertical swimming activity index is expressed in free vertical range units.

3.2.5. Periodicities in vertical movements

In order to detect periodicities in vertical movements of Atlantic cod, spectral analyses using fast Fourier transform were performed on depth time-series extracted from tags. The Fourier transform approximates a function with pairs of orthogonal sine and cosine terms and enables the detection of hidden periodicities in a complex signal as well as their relative importance (Chatfield, 1989). Long-term trends (seasonal, annual) were removed by fitting a second-order polynomial to the depth times-series prior to spectral analyses. Spectral analyses were performed on detrended time-series for each month using Matlab R2012a signal processing toolbox. A Hanning window was used to reduce spectral leakage. The Hanning window offers optimal balance between resolution of signal amplitude and signal frequency. Monthly analyses ensured a precise identification of periods during which periodic movements occurred. Depth time-series were finally visually inspected to confirm results from spectral analyses.

3.3. Results

3.3.1. Migratory behaviour

To date, 15 of the 353 DSTs implanted were recovered providing a collection of 5181 days of data. Recaptures concentrated along the Newfoundland west and southwest coasts (NAFO divisions 4R and 3Pn, Figure 3.1). At the beginning of the program no special warning message other than a traditional spaghetti tag was put on the back of tagged cod. Fishermen thus did not pay attention to internal DSTs while gutting fish, which resulted in the loss of 12 DSTs, as indicated by the serial numbers of recovered spaghetti tags. An extra 4 DSTs were recovered but data could not be downloaded due to technological failures. None of the fish tagged along the Québec North Shore (division 4S) were recaptured.

Two distinct behaviours appeared from reconstructed individual tracks (Figures 3.3 and 3.4). Ten fish were classified as migrants and three as residents (Table 3.1). The ten migratory individuals displayed relatively similar trajectories. They overwintered in the relatively deep (339 ± 88 m) and warm (5.3 ± 0.3°C) waters of the Laurentian Channel (Figures 3.3 and 3.5). Variation occurred among individuals in their winter depth and geographic distributions within the Laurentian Channel, however, winter temperatures were stable among and within individuals (Table 3.2, Figure 3.5). The spring was marked by an increase in the vertical swimming activity. Individuals migrated northward along the slopes of the Laurentian Channel, crossed the cold intermediate layer

in April-May, and reached coastal shallow waters (69 ± 38 m) of western Newfoundland in summer (Figures 3.3 and 3.5). Temperatures experienced in summer were colder and more variable (3.9 ± 2.6°C) than winter temperatures. The daily thermal range regularly reaches 10°C and above during summer (data not shown). Once again, variation occurred among individuals in the distance travelled from wintering to summer feeding areas and in the routes used to migrate. Individuals #13039 and #2400 spent the summer near the Strait of Belle Isle, several individuals spent the summer in the vicinity of Bonne Bay (#586, 12996, 12998, 13036 and 13388) and one individual spent the summer near St. George's Bay (#128). The fall was marked by migration back to the Laurentian Channel. In contrast with spring migration, fall migration was characterized by a low vertical swimming activity, despite a depth shift from shallow to deep waters (Table 3.2). Three individuals (#128, 12996 and 13036) were tracked for two years. They displayed similar migratory patterns between the two years (Figures 3.3c and 3.3d).

Three individuals displayed resident behaviour inside the Gulf along the west coast of Newfoundland. During the winter and early spring, they displayed prolonged periods of limited swimming activity in shallow (40 ± 15 m) and near-freezing (–0.9 ± 0.03°C) coastal waters (Table 3.2, Figures 3.4 and 3.5). Swimming activity increased in late spring, early summer. During summer and fall, they displayed localized movements in western Newfoundland (mean summer depth of 54 ± 14 m and temperature of 4.7 ± 2°C; mean fall depth of 37 ± 12 m and temperature of 4.8 ± 0.4°C).

Resident and migratory cod had common summer feeding areas but distinct overwintering areas. Migrants experienced higher temperatures than residents in winter and spring, but lower temperatures in summer and fall (Table 3.2). The increase in swimming activity, which followed the winter limited mobility, occurred in April and June for migrants and residents respectively (data not shown).

Two cod (#165 and 166) were tracked for only 54 days, from January 8 to March 3rd 2010, thus preventing any migratory behaviour inference (Table 3.1). These two cod overwintered in 1.3°C and 19 m deep water along the southwest coast of Newfoundland (division 3Pn). One individual (#166) was recaptured 209 days and 2 km away from the release. The other individual (#165) tagged in division 3Pn was recaptured 525 days after in division 3Ps (*i.e.* 222 km away), exemplifying the well-known mixing between the two management units.

3.3.2. Geolocation model error assessment

No true model validation using artificial fish was performed in this study. However, model accuracy was evaluated by looking at the residuals between daily maximum depth and associated temperature recorded by tags and bathymetry and bottom temperature inferred from estimated daily positions. Residual were first inspected visually for each individual tagged fish and then grouped together (Figure 3.6). More than 66% percent of the depth residuals were inferior to 5 m (Figure 3.6a) and more than 66% of temperature residuals were inferior to 0.65°C (Figure 3.6b), suggesting that the model performed well.

3.3.3. Periodicities in vertical movements

Spectral analyses and visual inspections of depth time-series revealed three types of periodic signals. First, periodic signals with a frequency of two cycles per day were identified (Table 3.3, Figure 3.7a). This semi-diurnal cycle resulted from the tidal signal and was observed when fish position was near or on the seabed (seabed association). Residents displayed semi-diurnal cycles during the long period of immobility in winter and early spring. Some migratory cod displayed semi-diurnal cycles during winter residency in the Laurentian Channel and at the end of summer while migrating, confirming that vertical activity is not necessarily correlated with horizontal activity (Hobson et al., 2009).

Periodic signals of one cycle per day revealed diel vertical migration (DVM). Two classes of DVM appeared: normal DVM (nDVM; dusk ascent – dawn descent, Figure 3.7b) and reverse DVM (rDVM; dawn ascent – dusk descent, Figure 3.7c). Seven of the nine migratory cod displayed nDVM in the spring while one resident cod displayed nDVM in early summer (Table 3.3). nDVM lasted for about one week to ten days. The height of nDVM approximated half the height of the water column (Figure 3.7b). Abrupt peaks were observable at dawn and dusk. rDVM were observed in two situations: in late spring and in the fall (Table 3.3).

3.4. Discussion

Reconstruction of Atlantic cod movements in the northern Gulf of St Lawrence resulted in the identification of both resident and migratory individuals. Resident cod, identified for the first time in the population, displayed a five month-long period of limited swimming activity in shallow waters (<100 m) along western Newfoundland. They experienced the seasonal gradual decrease of water temperature, which reached a minimum of –1.5°C in February and March. The swimming activity may be limited to avoid extra energetic expenditures while experiencing subzero temperatures. Similar to inshore resident cod from Trinity Bay, resident cod in the Gulf may synthesize antifreeze glycoproteins to limit overwinter mortality (Goddard et al., 1994).

Migratory individuals followed previously documented migration patterns in the northern Gulf of St Lawrence with discrete seasonal habitats. They appeared to actively seek deeper and warmer waters as overwintering areas, either to escape ice formation in the Gulf (Fréchet, 1990) or to facilitate vitellogenesis (Castonguay et al., 1999). Winter depth and temperature distribution were similar to those documented in previous studies, however, the geographic location within the Laurentian Channel slightly differed (Campana et al., 1999; Castonguay et al., 1999). This slight difference may result from the low horizontal depth and temperature gradients in the deep waters of the Laurentian Channel, which limited the accuracy of the geolocation when fish were distributed in the deep layers of the Laurentian Channel. Studies on the geolocation of Atlantic cod in

similar estuarine environments (*i.e.* the Baltic Sea) have used data loggers equipped with salinity probes (Andersen et al., 2007; Neuenfeldt et al., 2007). It is uncertain if salinity would improve geolocation accuracy in wintering areas because of the low horizontal salinity gradients in the Laurentian Channel deep water masses (Galbraith et al., 2012).

In the spring, migratory individuals were distributed along the slope of the Esquiman Channel near St George's Bay, where they displayed diel vertical migration with ascent at dawn and descent at dusk (nDVM). Combined acoustic, bottom trawl, and ichthyoplankton spring surveys have documented nDVM by spawning aggregation of cod at similar depth and location as the nDVM observed in this study (Ouellet et al., 1997; McQuinn et al., 2005). Experimental studies have showed that cod spawning behaviour is characterized by night ascent in the water column (Brawn, 1961; Hutchings et al., 1999). Detailed acoustic surveys have documented the formation of spawning columns at night by Atlantic cod (Rose, 1993; Fudge and Rose, 2009; Knickle and Rose, 2012). Hence, nDVM exhibited by migratory fish during the spring likely reveals the formation of spawning columns. Interestingly, one resident fish (#13663) displayed nDVM in the summer inside Bonne Bay, consistent with a delayed spawning induced by the subzero temperature experienced during the winter (Kjesbu, 1994; Smedbol and Wroblewski, 2002) and summer observations of spawning females in the area (chapter 4).

The summer inshore feeding migration was characterized by lower but more variable temperatures (3.9 ± 2.7°C) and by the occasional presence of reverse DVM

(ascent at dusk and descent at dawn). rDVM reflected movements across various layers of the stratified water column in coastal areas (*i.e.* from below to inside the cold intermediate layer and within the thermocline). rDVM in zooplankton species has long been recognised (Ohman et al., 1983). Recently, rDVM in basking shark (*Cetorhinus maximus*) has been linked to a foraging behaviour on zooplankton in inner-shelf areas near thermal fronts (Sims et al., 2005). rDVM in this study may reflect foraging behaviour on zooplanktivorous pelagic preys outside the Atlantic cod thermal preferundum (Rose and Leggett, 1989; Stensholt, 2001).

Migratory individuals displayed a homing behaviour to their summer feeding locations. Two of the three individuals tracked for two years homed to the same areas each year. These results confirm the recently documented homing behaviour up to three years after release in the population (Tamdrari et al., 2012a), as well as the multiyear homing behaviour documented on a spawning area in the neighbouring 3Ps population (Robichaud and Rose, 2001). Migration routes tended to follow the slopes of the Esquiman Channel, a known migratory corridor for Atlantic cod in the nGSL (McQuinn et al., 2005). This suggests that Atlantic cod may use bathymetric features as orientational cues for long-distance migration (Rose, 1993).

The identification of residents and migrants in the nGSL Atlantic cod population raises questions about the mechanisms that maintain the two alternative tactics in the population over evolutionary times. Are the two tactics maintained by some degree of

genetic isolation or by a conditional strategy? In Icelandic cod stock, resident coastal cod and migratory frontal cod show different *Pan* I genotypes maintained by fine-scale differences in spawning habitat selection (Pampoulie et al., 2008; Grabowski et al., 2011). Based on microsatellite DNA loci and electronic tagging studies, resident and migratory cod found in Kattegat have been shown to display philopatric behaviours with distinct population origins (Kattegat and North Sea respectively), although some straying occurs between the two populations (Svedäng et al., 2012). In eastern Newfoundland, aggregation of resident cod in Smith Sound show no differentiation for six microsatellite DNA with offshore cod from the Bonavista Corridor and the Halibut Channel suggesting that alternative migratory behaviours in that population may not result from genetic isolation (Rose et al., 2011).

In the northern Gulf of St Lawrence, traditional tagging (Yvelin et al., 2005), scale microchemistry analysis (Sagnol, 2007), and ichthyoplankton surveys (Bui et al., 2011) together suggested the existence of three subpopulations in NAFO divisions 4S, 4R, and 3Pn. In this study, resident and migratory cod were observed within the 4R putative subpopulation. Difference in the timing of DVM between resident and migratory cod seems to indicate some degree of temporal isolation in spawning between resident and migratory cod, which could result in genetic isolation (Kovach et al., 2010). Early spawning is traditionally associated with eggs and larvae dispersal and late spawning with retention (Bradbury et al., 2000; Runge et al., 2010). Spawning in the Gulf starts in the spring off St George's Bay but continues in early summer while cod migrate along the

west coast of Newfoundland (Ouellet et al., 1997; Méthot et al., 2005). Mixing hence potentially occurs between residents and migrants. Although not directly tested in this study, previous genetic studies based on Microsatellite DNA and the *Pan* I locus did not suggest any genetic isolation among cod in the nGSL (Ruzzante et al., 2000a; Sévigny et al., 2009). However, because of the large effective population sizes in Atlantic cod, the absence of genetic signal does not necessarily imply absence of population structure. The use of advanced genetic markers such as single-nucleotide polymorphisms (SNPs) may reveal genetic dimorphism between resident and migratory cod in the nGSL cod and explain the persistence of alternative migratory tactics as a result of a genetic determinism.

An alternative hypothesis to explain the persistence of the two migratory tactics in the population is the partial migration hypothesis (*i.e.* conditional strategy hypothesis). The adoption of one migratory tactic may depend upon a threshold level for environmental, developmental, and/or social cues. Juvenile white perch (*Morone americana*) spawned later in the season and characterized by higher growth rates have been shown to recruit preferentially as residents (Kerr and Secor, 2010). Consistent with timing of nDVM observed in this study, eggs, larvae, and juveniles of Atlantic cod in Newfoundland have been shown to originate from two main peaks of spawning activity, one in the spring and one in the summer (Methven and Bajdik, 1994; Bradbury et al., 2000; Knickle and Rose, 2010). Summer-spawned eggs and larvae experience higher water temperature and show faster development rates (Pepin et al., 1997; Bradbury et al.,

2000). Similarly to white perch, spring-spawned juvenile cod may preferentially adopt a migratory life cycle and summer-spawned juvenile cod a resident life cycle (Knickle and Rose, 2010). Alternative migratory tactics in Atlantic cod could thus be maintained by a conditional strategy, in which spawning time and early-life growth rate provide the proximate mechanisms that determine adult migratory behaviour. Further research is needed to test for this hypothesis.

3.5. Conclusion

By reconstructing movements of fish equipped with data-storage tags, we demonstrated that the northern Gulf of St Lawrence Atlantic cod population comprises a mixture of resident and migratory individuals. The two alternative migratory behaviours had distinct habitats in winter and early spring but overlapping habitats in late spring and summer. Whether the two tactics reflect within population or among population difference in migration propensity remains unclear. Provided there are further recoveries of DSTs, the combination of advanced genetic markers such as SNPs with the reconstruction of migration trajectories may provide new insight into the ecological and evolutionary factors that affect nGSL cod migration propensity. Finally, this research underlines the need to consider alternative migratory behaviours in the assessment and the management of the collapsed population. Indeed, spatial management measures may disproportionally

protect individuals from the population depending upon their migratory behaviour and the design of the management measures.

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Tables

Table 3.1. Tagging and recapture information for 15 Atlantic cod tagged with data-storage tags. FL: fork length, M: migratory, R: resident, U: undetermined. Distance corresponds to the distance between tagging and recapture locations. * Individuals for which the tag stopped recording before the recapture date.

		Tagging				Recapture				Days		
Fish ID	Tag Series	Date	FL (cm)	Latitude (°N)	Longitude (°W)	Date	FL (cm)	Latitude (°N)	Longitude (°W)	of data	Distance (km)	Behaviour
12996	LTD_1100	21 Sep 2007	65	49°37'	57°58'	06 Oct 2009	71	49°39'	58°00'	746	4	M
12998	LTD_1100	26 Sep 2007	58	49°37'	57°58'	22 Aug 2008	63	49°37'	58°58'	331	1	M
13012	LTD_1100	21 Sep 2007	63	49°37'	57°58'	10 Jul 2008		51°06'	57°08	293	175	R
13036	LTD_1100	26 Sep 2007	49	49°37'	57°58'	22 Jul 2009	57	49°26'	58°20'	665	35	M
13039	LTD_1100	18 Aug 2007	60	51°26'	56°36'	02 Aug 2008	62	51°37'	55°29'	350	79	M
13363	LTD_1100	31 Oct 2008	55	49°37'	57°58'	21 Sep 2009		49°42'	58°04'	325	11	R
13380	LTD_1100	31 Oct 2008	61	49°37'	57°58'	30 Jul 2009	65	49°30'	58°09'	272	18	R

13388	LTD_1100	23 Sep 2008	71	49°28'	57°54'	30 Jul 2009	73	49°31'	57°55'	310	6	M
128	LTD_1400	07 Nov 2008	53	47°51'	59°27'	26 Oct 2010	56	47°34'	58°44'	718	62	M
423	LTD_1400	07 Nov 2008	72	47°51'	59°27'	19 Jun 2009	74	49°26'	58°14'	224	197	M
586	LTD_1400	31 Oct 2008	53	49°37'	57°58'	14 Nov 2009		49°36'	58°00'	348	4	M
2400	LTD_1400	03 Aug 2011	58	50°17'	57°47'	06 Jul 2012	63	50°18'	57°37'	338	12	M
165*	LTD_1500	08 Jan 2010	60	47°35'	58°55'	17 Jun 2011	70	47°35'	55°57'	54	120	U
166*	LTD_1500	08 Jan 2010	48	47°35'	58°55'	05 Aug 2010	50	47°35'	58°53'	54	2	U
167*	LTD_1500	01 Oct 2009	49	50°42'	57°26'	17 Aug 2010	52	50°46'	57°20'	153	10	M

Table 3.2. Mean depth, temperature, and vertical swimming activity index (see text for details) for migratory (n = 10) and resident (n = 3) cod. Numbers in brackets show standard deviations.

	Winter	Spring	Summer	Fall
		Depth (m)		
Migratory	339 (88)	154 (68)	69 (38)	140 (56)
Resident	40 (15)	41 (14)	54 (14)	37 (12)
		Temperature (°C)		
Migratory	5.3 (0.3)	3.2 (1)	3.9 (2.6)	4 (0.7)
Resident	-0.9 (0.03)	1.4 (0.5)	4.7 (2)	4.8 (0.4)
		Swimming Activity		
Migratory	0.08 (0.07)	0.5 (0.2)	0.3 (0.2)	0.2 (0.1)
Resident	0.06 (0.05)	0.2 (0.2)	0.1 (0.1)	0.1 (0.1)

Table 3.3. Summary of periodic signals observed in depth time-series extracted from data-storage tags. nDVM = normal diel vertical migration (dusk ascent – dawn descent). rDVM = reverse diel vertical migration (dawn ascent – dusk descent). Seabed = seabed association.

FISH ID	nDVM	rDVM	Seabed
12996	Apr	Jun	-
12998	-	-	-
13036	May	Jun & Oct	Feb-Apr
13039	Apr	May	Sep
13388	Apr	-	-
128	Jul	Dec	-
423	May	-	-
586	Apr-Jun	-	-
2400	May	-	-
167	-	-	Jan
13012	-	Nov	Dec-May
13363	Jul-Aug	-	Nov-Apr
13380	-	-	Dec-Apr
165	-	-	Jan-Mar
166	-	-	Jan-Mar

Figures

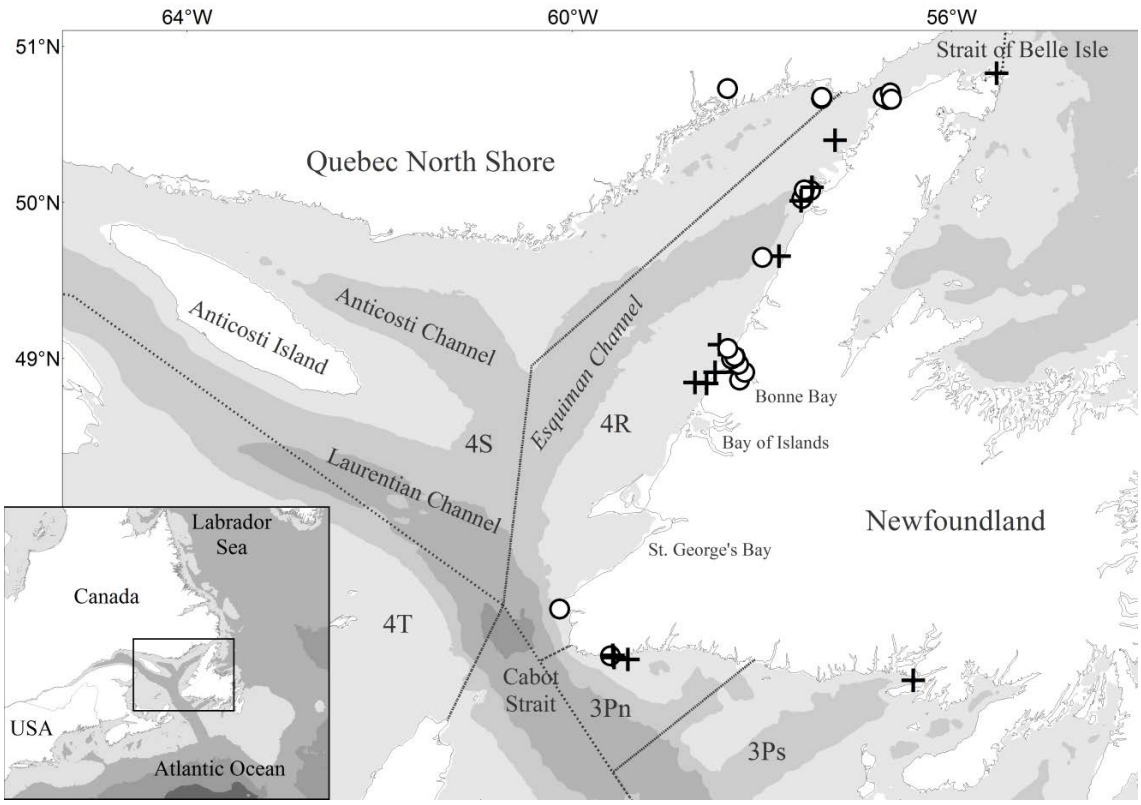

Figure 3.1. Map of the Gulf of St Lawrence with cod tagging (circles, n = 353) and recapture (crosses, n = 15) locations. The dotted lines delimit the Northwest Atlantic Fisheries Organization management units. Grey contours on the main map show 200-, 400- and 500-m isobaths.

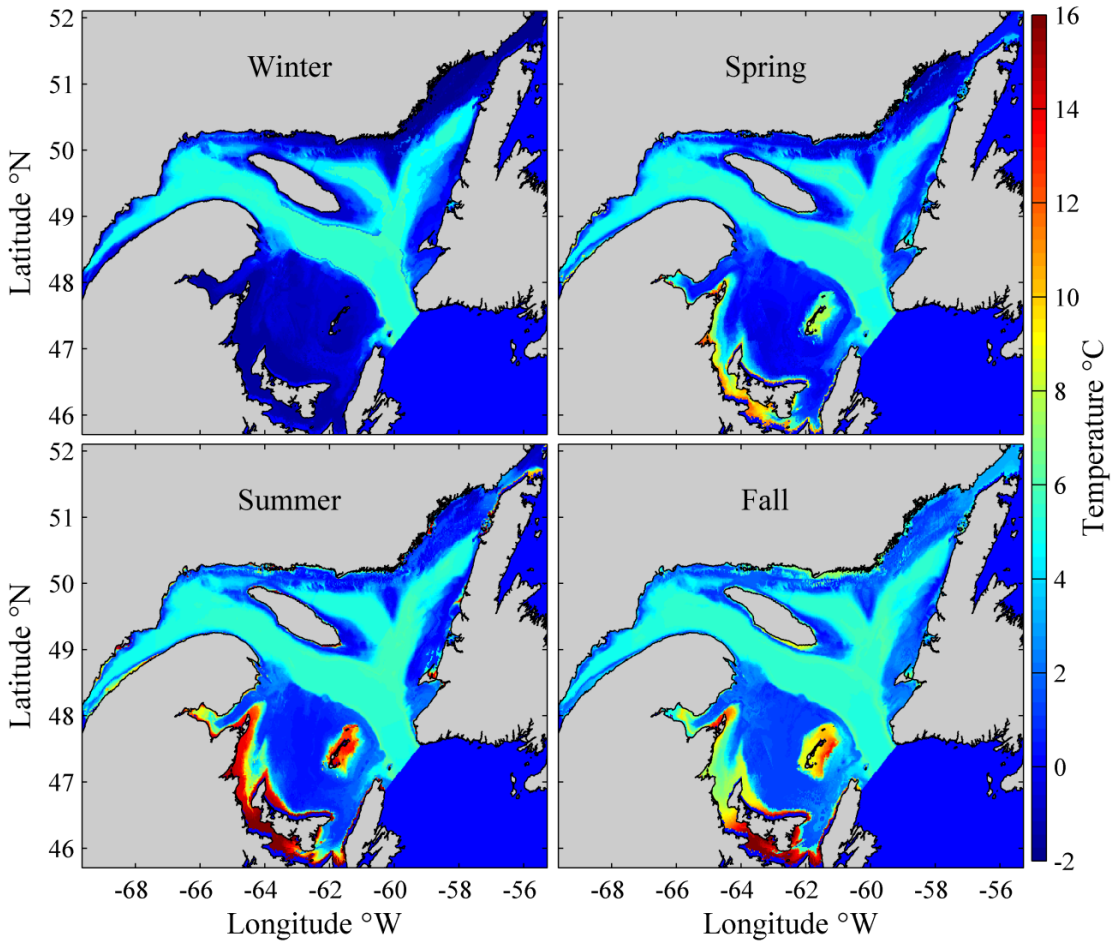

Figure 3.2. Quarterly bottom temperatures in the Gulf of St Lawrence in 2011.

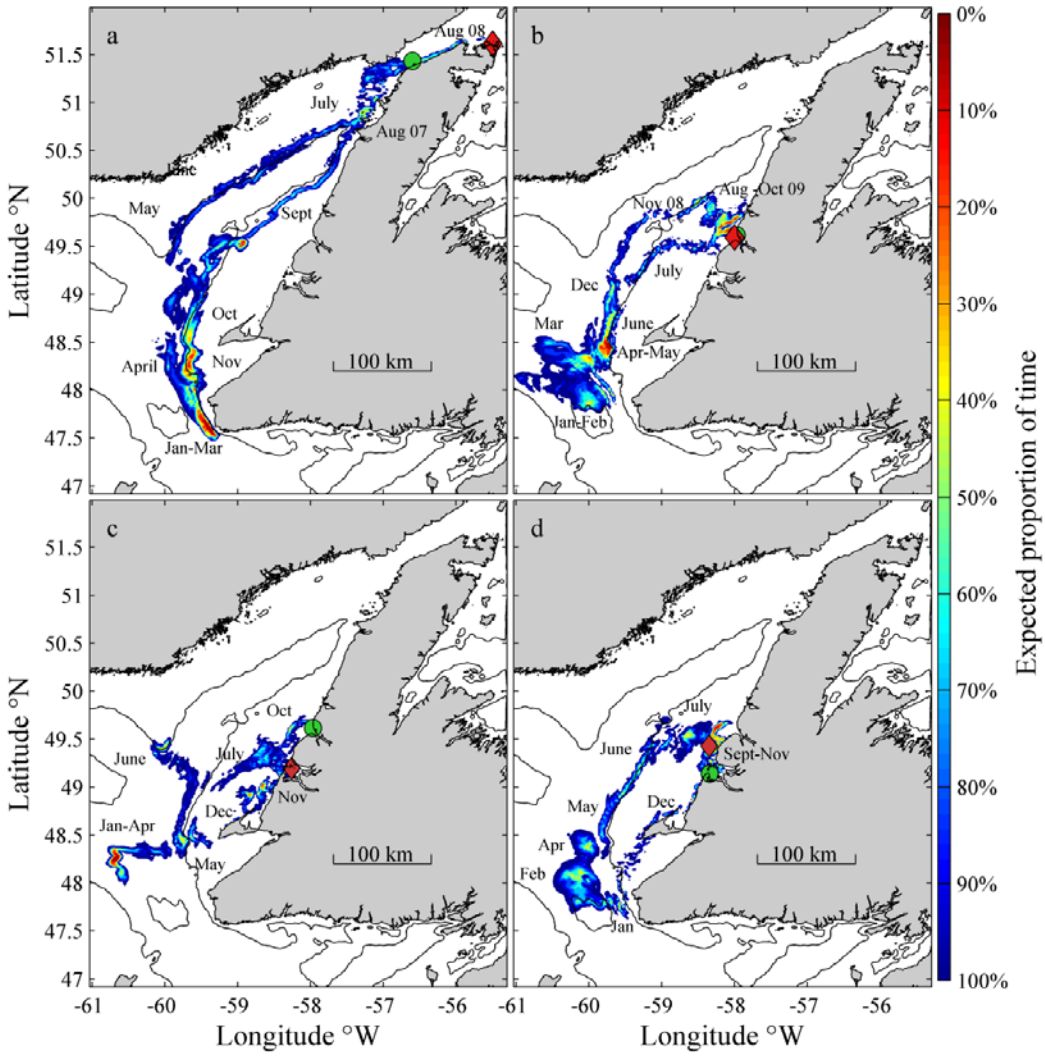

Figure 3.3. Spatial distributions of three migratory Atlantic cod. Contour bar shows the expected proportion of time spent in the contour area. Black lines show 200- and 500-m isobaths. Circles show initial positions and diamonds show final positions. (a) Cod #13039 from 18 August 2007 to 02 August 2008; (b) Cod #586 from31 October 2008 to 14 November 2009; (c) Cod #13036 from 26 September 2007 to 23 August 2008; (d) Cod #13036 from 24 August 2008 to 22 July 2009.

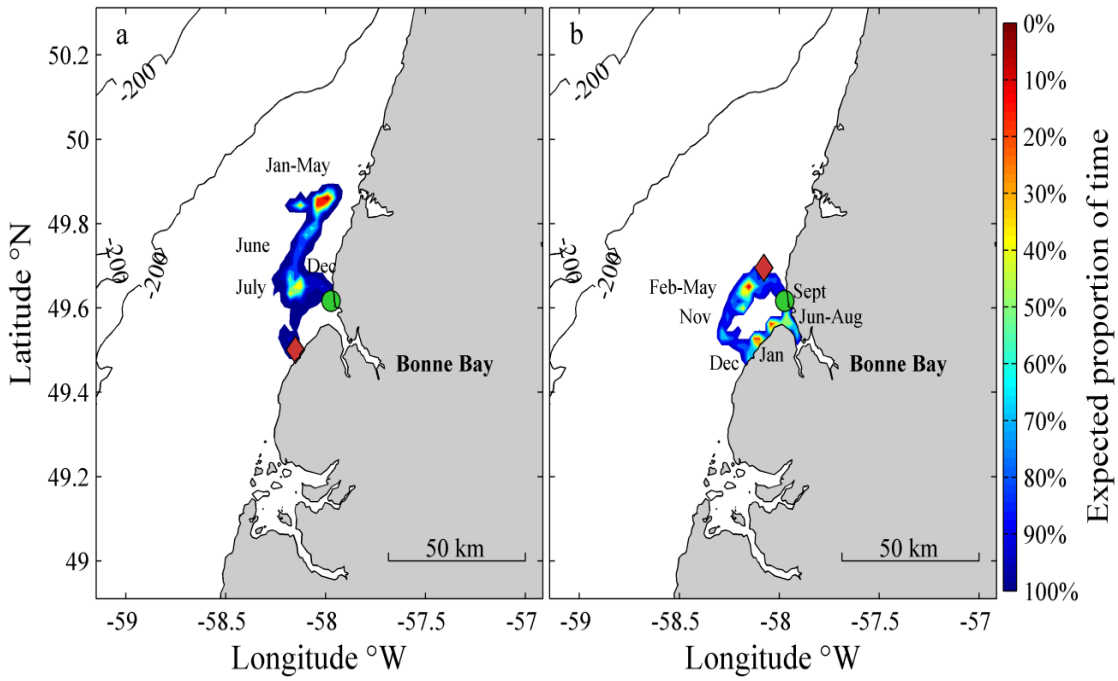

Figure 3.4. Spatial distributions of two resident Atlantic cod. Contour bar shows the expected proportion of time spent in the contour area. Blackline shows 200-m isobath. Circles show initial positions and diamonds show final positions. (a) Cod #13380 from 31 October 2008 to 30 July 2009; (b) Cod #13363 from 31 October 2008 to 21 September 2009.

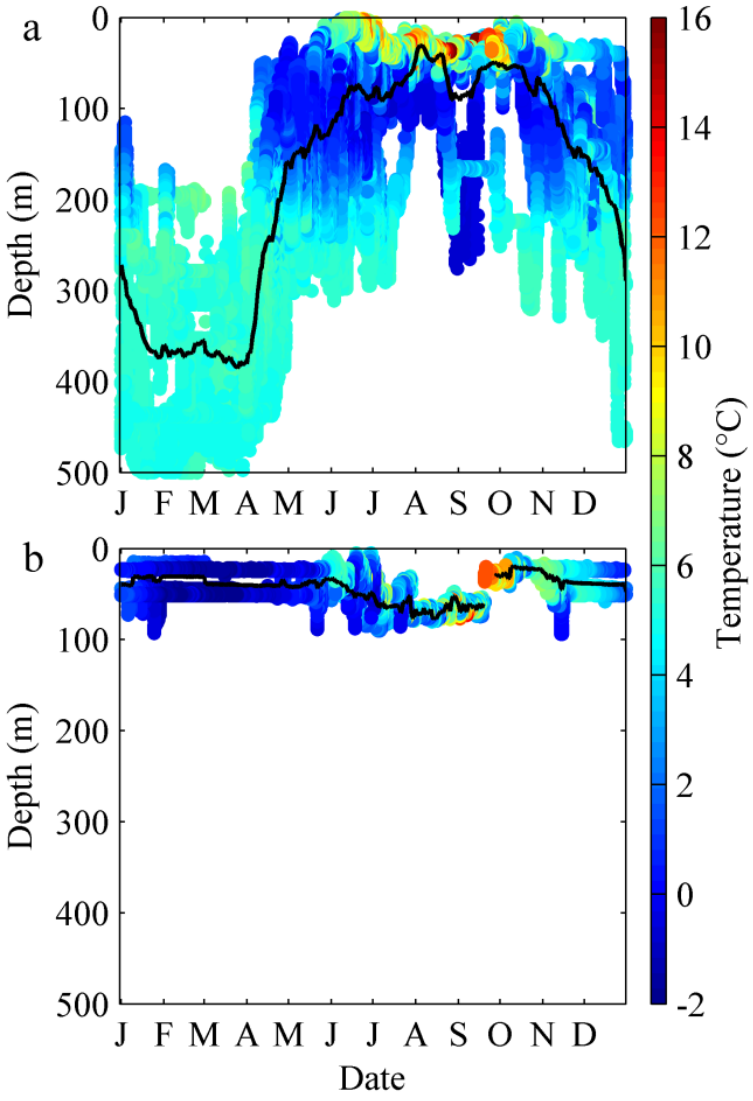

Figure 3.5. Depth and temperature profiles for (a) migratory cod (n = 10), and (b) resident cod (n = 3). Black lines show average depth.

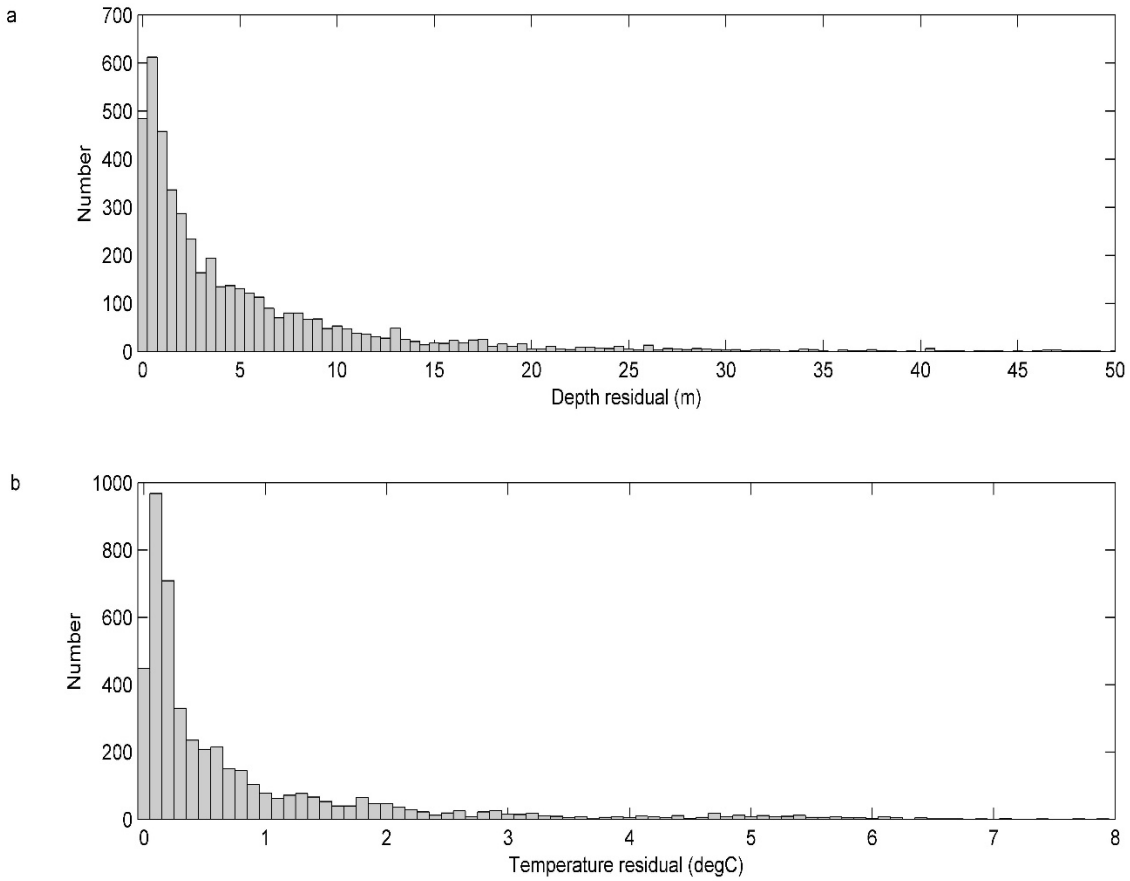

Figure 3.6. Frequency distributions of the residuals. (a) Depth; (b) Temperature.

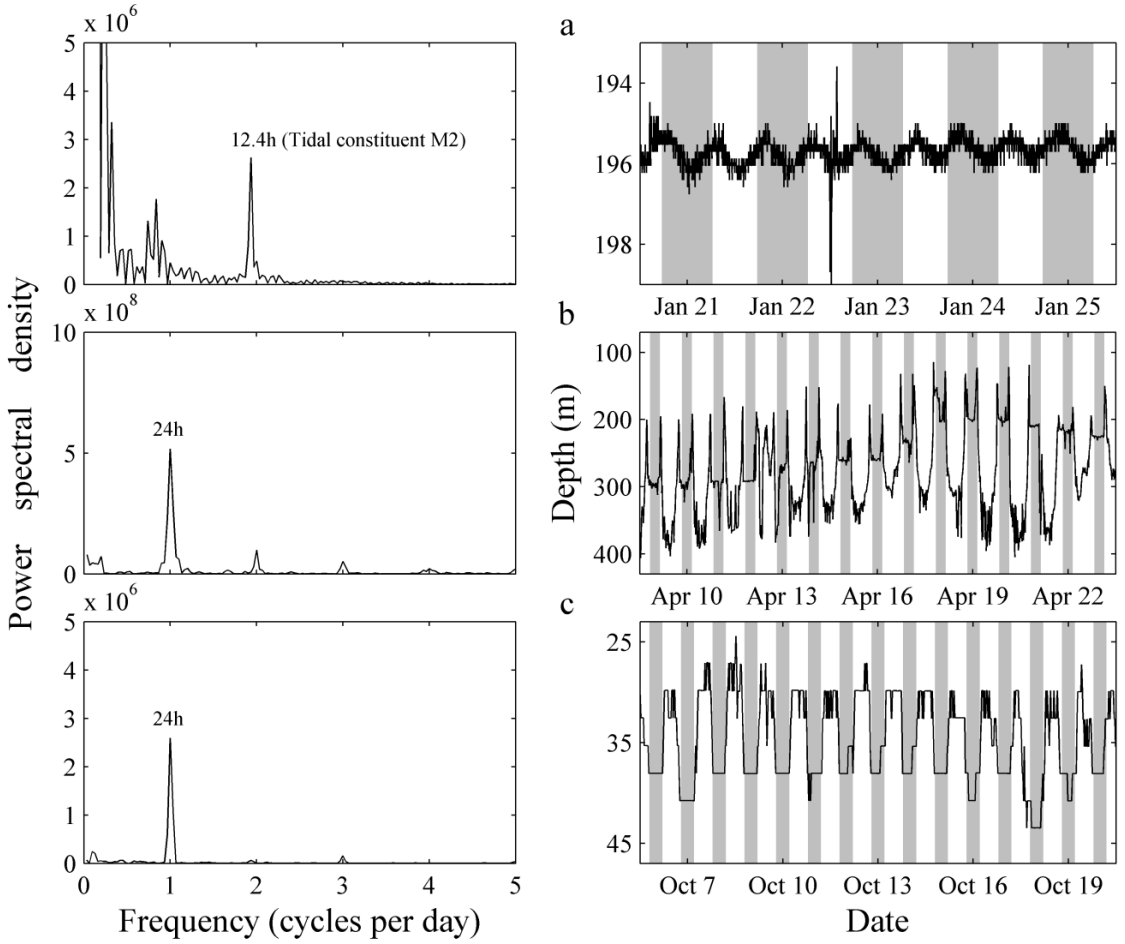

Figure 3.7. Periodograms (left) obtained from spectral analysis of depth time-series with corresponding depth profiles (right). Shaded areas indicate night-time. Note changes in scales. (a) Cod #167 displaying seabed association in January 2010; (b) Cod #586 displaying normal diel vertical migration in April 2009; (c) Cod #13036 displaying reverse diel vertical migration in October 2008.

Chapter 4. Adult and Juvenile Cod Distribution within the Fjord of Bonne Bay, and their Relation to Cod from the Gulf of St. Lawrence.

Abstract

Inshore waters provide nursery areas for juvenile Atlantic cod and support abundance of adults throughout the species geographic range. In the northern Gulf of St. Lawrence, surprisingly little is known about abundance and distribution of adult and juvenile cod in inshore waters along western Newfoundland. An electronic tagging experiment previously revealed that adult Atlantic cod exhibit year-round residency and a homing behaviour to the Bonne Bay area. In this study, I combined data from a 10 year long nearshore fish fauna survey performed with several sampling gear, with data on maturity, length-at-age, fishery landings, and genetics to evaluate the abundance and distribution of adult and juvenile cod in Bonne Bay, and to examine if the observed site-fidelity to the Bonne Bay area by adult cod led to the formation of a local population. Length frequencies revealed that all size classes, from newly settled juveniles to adults, were present in Bonne Bay. Abundance data suggested that adult cod were not abundant in Bonne Bay. Summer spawning and fall juvenile settlement indicated local recruitment. Settlement of age 0+ cod was not found to be associated with a specific habitat within the bay. The absence of genetic differentiation between cod from Bonne Bay and from the

northern Gulf at 11 microsatellites and at the *Pan* I locus, as well as the prevailing winds favoring advection of cod pelagic stages into Bonne Bay, suggested that external sources of recruitment are substantial. I concluded that the fjord of Bonne Bay does not appear to harbour a demographically or a genetically independent population of Atlantic cod. It however provides a nursery and a spawning area for Gulf cod. As such, Bonne Bay may help in the rebuilding of the collapsed population, which has been impeded by poor recruitment.

4.1. Introduction

Marine fish populations were once regarded as large panmictic (*i.e.* randomly and freely interbreeding) open populations, owing to the apparent absence of barriers to migration and dispersal (Hjort, 1914). Increased evidence for genetically distinct units at fine spatial scales have resulted in a paradigm shift towards temporally stable fine-scale populations (Hauser and Carvalho, 2008). This paradigm shift has not been accompanied by a similar shift in the scales of fish stock management, thus resulting in increasing mismatches between scales of demographic processes and management units (Reiss et al., 2009). To not adequately acknowledge small-scale population structures in fisheries management may lead to the extirpation of the less productive and more accessible local populations (Smedbol and Stephenson, 2001; Svedäng et al., 2010).

In the relatively continuous marine environment, local self-sustaining populations arise in areas where local recruitment dominates over external sources (Strathmann et al., 2002; Jorde et al., 2007). Adult residency and homing to spawning areas can promote local recruitment, if it results in segregation of spawning groups, if spawning products are retained on natal sites (Cowen et al., 2000), and if local density-dependent and stochastic processes increase growth and survival of juveniles (Houde, 1989; Bjornstad et al., 1999; Fromentin et al., 2001).

Coastal embayments, especially glacially carved fjords[3], facilitate the formation of local populations of marine fishes. Physical (presence of shallow sill) and hydrographic (estuarine circulation with surface outflow) barriers restrict external inputs of pelagic stages (Knutsen et al., 2007; Ciannelli et al., 2010), and limit adult movement (Green and Wroblewski, 2000; Espeland et al., 2008). Numerous local populations of Atlantic cod have been documented in fjords along the Norwegian coast (Knutsen et al., 2003; Jorde et al., 2007), as well as in the fjord of Gilbert Bay (Ruzzante et al., 2000b), in Smith Sound Trinity Bay (Smedbol and Wroblewski, 1997), and in Placentia Bay (Bradbury et al., 2008).

[3]A fjord is defined in this study following Farmer and Freeland (1983), as a coastal geological structure that possesses the three following characteristics i) longer than wider, ii) steep sided and deep, and iii) basin(s) separated by submarine sill(s).

Depth, salinity, temperature, and wave exposure gradients in coastal embayments induce a diversity of substrates and habitats available for juvenile Atlantic cod to settle. Juvenile cod display active selection towards the structurally complex habitats that enhance food availability and provide refuge from predators (Gotceitas et al., 1997; Renkawitz et al., 2011). In Smith Sound Trinity Bay, maximum densities of juvenile cod have been found in eelgrass bed of intermediate densities (Thistle et al., 2010). On Georges Bank, juvenile cod have been shown to prefer gravel to sandy bottoms (Lough, 2010).

In the Atlantic cod population from the northern Gulf of St. Lawrence (NAFO divisions, 3Pn4RS, Figure 4.1), poor recruitment and the demise of spawning components are two hypotheses proposed to explain the lack of recovery of the population (Swain and Castonguay, 2000; Smedbol et al., 2002; Duplisea and Robert, 2008; Chassot et al., 2009). However, surprisingly little is known about abundance and distribution of adult and juvenile cod in inshore waters along western Newfoundland, where the biomass has contracted in range (Tamdrari et al., 2010). Knowledge on juvenile cod distribution has been limited to bottom-trawl research surveys, which do not sample the shallowest juvenile habitats. Furthermore, studies on population structure have not considered inshore waters (Campana et al., 1999; Ruzzante et al., 2000a; Sagnol, 2007). In contrast, studies based on traditional fishers' knowledge have suggested that several fjords and bays along western Newfoundland, including St. George's Bay, Bay of Islands, Bonne

Bay, and St. Pauls inlet, may support local cod populations (Goose et al., 2003; Murray et al., 2008), but no study has further tested this hypothesis.

Reconstruction of migration routes of adult cod equipped with data-storage tags has revealed year-round residency and a homing behaviour to the fjord of Bonne Bay (chapter 3). An inshore fish sampling every June since 2002 has consistently revealed the presence of juvenile cod in Bonne Bay. The shallow waters of Bonne Bay are characterized by a great diversity of substrate and habitats (Hooper, 1975), which may facilitate juvenile settlement and enhance post-settlement growth and survival. Using multiple sources of data, this study aimed to examine whether: i) Bonne Bay supports a high abundance of adult and juvenile cod, ii) Bonne Bay harbours a genetically isolated population of cod, and iii) higher abundances of juvenile age-0 cod are associated with specific habitat types within the Bay.

4.2. Material and Methods

4.2.1. Study area

Bonne Bay is a sub-arctic fjord surrounded by the Gros Morne National Park on the west coast of Newfoundland, Canada (49° 30'N, 57° 52'W, Figure 4.1). It was excavated by multiple glaciers, but mainly originated during the retreat of the Laurentide Ice Sheet about 13,500 years ago (Shaw, 2003). Bonne Bay consists of two distinct basins: the

outer basin, composed of South Arm, and the inner basin, composed of East Arm and Deer Arm (Figure 4.2a). The outer basin is about 22 km long, has a maximum depth of 140 m, and is separated from the Gulf of St. Lawrence by a 35 m deep moraine. The inner basin is about 12 km long, has a maximum depth of 230 m, and is separated from the inner basin by a 14 m deep sill (Figure 4.2b). The total surface area approaches 80 km^2. There are two main sources of freshwater draining off the boreal forested watershed into the bay: Deer Brook and Lomond River. The combined freshwater discharge from the two watersheds is less than 0.5% of the water volume contains annually in Bonne Bay (Tian et al., 2001). The nearshore zone of Bonne Bay varies in bottom substrate type, bottom slope, vegetation coverage, seawater temperature and salinity (Hooper, 1975).

Similar to other Fjords, water circulation in Bonne Bay is governed by three major forcings: freshwater, tidal, and wind forcings. Pressure gradients induced by freshwater inputs result in a traditional two-layer circulation system over the inner sill: an outflow of low saline water in the upper layer and an inflow of saline water from the Gulf of St. Lawrence in the lower layer (Richards, 2005; Peng, 2008). Due to vertical and lateral constrictions at the sill, tidal forcing induces severe variations in the two-layer circulation system. The ebb phase of the tide is accompanied by an increase of the upper layer outflow. The amplitude of the upper layer outflow decreases with depth to the point where it reverses near the bottom. The flood phase is accompanied by an increase of the bottom layer inflow to the point where it overcomes the surface freshwater outflow (Peng, 2008). Finally, friction forces induced by the wind on the surface layer (*i.e.* wind stress)

may accelerate or decelerate top-layer outflow, depending upon wind direction. High coherence between wind stress and through channel flow velocity has been observed in Bonne Bay (Richards, 2005).

Temperature across the sill is characterized by marked seasonal changes (Figure 4.3). Heat loss to the atmosphere induces a decrease in water temperature below 0°C throughout the water column from February to April. In late summer, the water temperature over the sill is about 16-18°C. Bonne Bay surface layer warms in the spring and cools in the fall quicker than the Gulf of St. Lawrence waters because the relatively low quantities of freshwater draining into Bonne Bay respond quicker to seasonal changes in atmospheric temperature than the larger quantities of seawater.

4.2.2. Sampling design

A nearshore fish fauna survey was conducted at daylight for two weeks each June from 2002 to 2011 at seven sites in East Arm Bonne Bay (Figure 4.2a). The fish collection sites were chosen to represent the range of nearshore habitats available in the bay. Site 1 is a sheltered cove near the inner sill. Site 1 has a pebble beach and a subtidal bottom substrate of sand and silt with scattered boulders. Site 1 is inhabited by various patchy seaweeds species such as *Polysiphonia* spp. and beds of blue mussels (*Mytilus edulis*). Site 2 is an exposed cove in East Arm. Site 2 has a pebble and cobble beach with scattered boulders. The subtidal substrate is hard with sand, pebbles and scattered boulders. Patchy brown seaweeds cover the seafloor. Site 2A is an exposed cove with a

steeper bottom slope than nearby Site 2. Site 3 is the river delta at the mouth of Deer Brook. The beach at Site 3 is composed of sand, granules and pebbles. The subtidal substrate at Site 3 is sand and silt. Eelgrass beds (*Zostera marina*) are present at Site 3. Site 3A is a barachois, *i.e*. a shallow (< 2 m deep) lagoon separated from the Deer Brook river delta by a sand bar. The bottom substrate of the barachois exposed at low tide is composed of sand and silt. Site 4 is an exposed cove at the inner end of East Arm. The beach substrate at Site 4 consists of cobbles with some pebbles and scattered boulders. The subtidal substrate is a mixture of pebbles, sand and silt. Patches of eelgrass are present in the sub-tidal zone of Site 4. Site 4A is the delta of the Lomond River. The beach substrate at Site 4A consists of granules and sand with some pebbles. The subtidal substrate is sand and silt and a wide eelgrass meadow is present. Depth and salinity profiles at each site are provided in Appendix C.

Several fish sampling gears were used to overcome bias in population density and length frequency estimations induced by gears selectivity (Methven and Schneider, 1998). Sampling gears included a 10 m and a 25 m beach seine, a 4.9 m semi-balloon bottom trawl, and various mesh size gillnets (1, 1.5, 2, and 3 inches). A detailed description of the sampling gears and their deployment is available in Currie et al. (2009). All Atlantic cod collected during the survey were measured to the nearest millimetre standard length (SL). Juvenile Atlantic cod (*Gadus morhua*) were distinguished from juvenile Greenland cod (*Gadus ogac*) by the absence of pigmentation on the tip of the second anal fin (Dr. David Methven, pers. comm.). An additional sampling was performed in October 2009 using a

25 m beach seine to investigate the settlement of juvenile cod in Bonne Bay during the fall. A detailed account of all the sampling sets is provided in Table 4.1. Finally, adult cod were sampled in collaboration with Bonne Bay commercial fishermen using commercial 6 inches mesh size gillnets in South Arm Bonne Bay for two weeks in July 2009 and July 2010. Fish were measured, otoliths were removed to age individuals, and sexual maturity stages were determined for females.

4.2.3. Environmental data

Water column profiles of seawater temperature and salinity were recorded at each site before deployment of fish collection equipment (Figure 4.3). Salinity and temperature were measured using a YSI® Model 30M-100FT water quality probe. Bottom depth was measured using a dual beam depth sounder. Wind speed and direction recorded at the Rocky Harbour weather station were obtained for the year 2009 and 2010 from the Canadian National Climate Data and Information Archive. Wind stress was calculated following Large and Pond (1981), assuming that the wind speed recorded at the weather station equalled the wind speed at 10 m above the water surface.

4.2.4. Analysis of maturity

Female Atlantic cod have a shorter spawning window than males, thus inference of spawning time and location from maturity analysis of female cod are more accurate (Hutchings and Myers, 1993). Sexual maturity stages were visually determined following Morrison (1987): i) immature: small and firm ovaries; ii) maturing: larger cream-colour

ovaries, visible opaque eggs; iii) spawning: presence of translucent eggs; and iv) spent: shrunken soft and flabby ovaries.

4.2.5. Genetic analysis

Adult and juvenile Atlantic cod collected in East Arm Bonne Bay in 2009 were genotyped at 11 microsatellites loci and at the Pantophysin locus (*Pan* I) and compared with the genotype from cod sampled in the Gulf of St. Lawrence in 2002, 2005, and 2007 (Figure 4.1). The number of genotyped cod from Bonne Bay and from the GSL was respectively 59 and 139 for microsatellites, and 55 and 144 for the *Pan* I locus (details on tissues and DNA extractions are available in Sévigny et al., 2009). *Pan* I is a protein coding gene thought to be under selection in Atlantic cod (Pogson and Mesa, 2004). Microsatellites are putative neutral markers exhibiting high polymorphism. They are used to identify population structure.

Observed (*Ho*) and expected (*He*) within sample heterozygosity were computed using software ARLEQUIN V3.5.1 (Excoffier and Lischer, 2010). Within sample departure from Hardy-Weinberg equilibrium (F_{IS}) was estimated using FSTAT v2.9.3.2 (Goudet, 2001). Variances in allelic frequencies were used to estimate fixation index F_{ST} between Bonne Bay and GSL. F_{IS} and F_{ST} were tested for significant differences from zero using 1000 randomizations. For microsatellite data, allelic richness per locus (*Arich*) was estimated within samples using the rarefaction approach implemented in ADZE v1.0 (Szpiech et al., 2008). Differences in *Arich* between Bonne Bay and GSL samples were

tested for statistical significance using the Wilcoxon test. Allelic frequencies instead of allelic richness were reported for the *Pan* I locus because the same two alleles (*Pan* I^A and *Pan* I^B) were present.

4.2.6. Population dynamics

Assuming that Bonne Bay supports a self-sustaining population of Atlantic cod, a Schaefer model was constructed to estimate the biomass of adult cod in Bonne Bay. The model formulation was:

$$B_{t+1} = B_t + rB_t\,(1 - B_t / K) - C_t \qquad (4.1)$$

where B_t is the biomass at year *t*, r is the intrinsic growth rate of the population, *K* is the carrying capacity of the ecosystem, and C_t represents the catches at year *t*. Landings from Norris Point and Woody Point were used as catch data. A carrying capacity of 550 tons was estimated using Robichaud and Rose (2004) linear relationship between maximum historical biomass and surface area of the bay. The von Bertalanffy growth curve with a fixed maximum length parameter (Raper and Schneider, 2013) of 800 mm was fitted to length-at-age data to estimate individual growth rate (Figure 4.4). The fitted von Bertalanffy growth curve indicated a growth rate of 0.19 y^{-1}. Individual growth rate and population intrinsic growth rate are different parameters. Nevertheless, the individual growth rate obtained from the von Bertalanffy growth curve was found consistent with population intrinsic growth rates from Haedrich and Hamilton (2000) and Hu and

Wroblewski (2009). It was thus used in the Schaefer model. The model was computed for the years 1994 to 2011. An initial biomass of 110 tons (20% of K) was considered conservative because the model initial year corresponded to the first year of the moratorium on cod fishery in the Gulf (at that time the estimated spawning stock biomass for the nGSL cod was below 10% of its historical maximum level; Fréchet et al., 2009).

4.2.7. Habitat association of juvenile cod

The nearshore fish fauna survey of Bonne Bay provides information on the habitats occupied by juvenile Atlantic cod in the bay. The 25 m beach seine data for age-0 juvenile cod (defined as individuals ≤ 96 mm SL; Methven and Schneider, 1998) were analyzed to determine if there was a relationship between sampling site (*i.e.* habitat type) and abundance of juvenile cod in East Arm Bonne Bay. Only two juvenile cod were caught using the 10 m seine over the ten years of sampling; therefore, data collected with the 10 m seine were not included in the analysis. For consistency, specimens collected with the 25m seine in October 2009 were also excluded. The effect of location (Site 2, 2A, 3, 4 or 4A) and year (sampling during June in the years 2002 to 2011) on the number of age-0 cod caught per tow were analyzed using a two-way Analysis of Variance (ANOVA) within the General Linear Model (GLM) approach. The null hypothesis was that sampling site and sampling year did not affect the number of age-0 cod caught per tow of the 25 m beach seine. Two GLMs were constructed. The first GLM incorporated sampling site and year of collection as explanatory variables:

$$N = \beta_O + \beta_S S + \beta_Y Y + \varepsilon \quad (4.2)$$

where N is the number of age-0 cod caught per tow, S represents the sampling site, Y represents the year of collection, and $\varepsilon \sim N(0, \sigma^2)$ is the residual error, which follows a normal distribution of mean 0 and standard deviation σ^2. In this case, the year variable was considered categorical, which allows testing for habitat effects controlled for year. The interaction term, which tested whether habitat effects depend on year, could not be evaluated as there were no tows conducted at certain sampling sites in some years (Table 4.1). A second GLM was constructed to test for temporal trends:

$$N = \beta_O + \beta_S S + \beta_Y Y + \beta_{SY} SY + \varepsilon \quad (4.3)$$

where variables are defined as above, except that year is a continuous variable instead of a categorical variable. This model tested for trends. In this second model, the interaction between site and the decade sampling period could be considered and evaluated. The criterion for significance (α value) was set at 0.05 for all tests. For both models, residuals were examined for normality and homogeneity (Sokal and Rohlf, 2012 4th ed.). Neither of the two GLMs met the assumptions of normality of residuals and of homoscedasticity; therefore, randomization tests were performed to calculate more accurate p-values. New F-ratios were calculated by randomly permuting residuals 5000 times (Anderson, 2001). New p-values were then obtained by calculating the proportion of F-ratios higher or equal the originally observed F-ratio. GLM and randomization tests were performed using the *GeneralizedLinearModel* function in Matlab R2012a.

4.3. Results

4.3.1. Size range of collected cod

All size-classes of Atlantic cod from the newly settled juvenile stage to the adult spawning stage were collected in Bonne Bay. The 676 cod ranged from 23 mm to 800 mm SL, and from 0 to 10 years old (Figure 4.5). Age-0 cod dominated the size frequency of cod collected. The size distribution of cod caught was heavily influenced by the selectivity of sampling gears. The 25 m beach seine predominantly caught individuals smaller than 100 mm, whereas multi-panel gillnets selected for 200 mm individuals, 3" mesh size gillnets for 300-350 mm individuals, and 6" mesh size commercial gillnets for 500-600 mm SL (Figure 4.6). Catch per unit of effort revealed low abundance of Atlantic cod in East Arm Bonne Bay with an average of 2.29 individuals caught per tow of 25 m beach seine (Table 4.2), and 0.24 individuals caught per hour of immersion of gillnets (Table 4.3). Otolith readings revealed the presence of the first winter annuli for juvenile cod caught in June and ranging in size from 66 to 96 mm SL. Length-at-age keys in the northern Gulf of St. Lawrence show that one year old juveniles measured between 130 and 250 mm (DFO, unpublished data). This suggests that 66 to 96 mm juvenile caught in June in East Arm Bonne Bay were young of the previous fall. Sampling in October 2009 revealed the presence of small juvenile cod ranging in size from 26 to 42 mm SL, suggestive of a fall settlement in East Arm Bonne Bay.

4.3.2. Environmental data

Analysis of the wind record in Rocky Harbour showed that both eastward and northward component of the wind stress were lower from late spring to early fall than during the rest of the year (Figure 4.7). Interestingly, wind stress direction differed between the spring and the summer. The wind stress component directed towards the southwest in spring 2009 and 2010 disappeared in summer 2009 and 2010 (Figure 4.8).

4.3.3. Maturity analysis

Catch of spawning females at the vicinity of the inner sill in South Arm Bonne Bay in early July 2009-2010 indicated that summer spawning occurred in Bonne Bay. Among the 112 females sampled, 8 (7%) were identified as immature, 13 (11%) as maturing, 25 (22%) as spawning, and 66 (59%) as spent. Males in spawning condition were also observed during sampling but were not recorded.

4.3.4. Genetic analysis

Observed heterozygosity from microsatellites was high for both GSL and Bonne Bay samples with values of 0.65 and 0.677, respectively. F_{IS} value for the GSL sample indicated significant heterozygote deficit. Allelic richness was similar for the GSL and Bonne Bay sample (*Arich* = 10.1 for both samples). F_{ST} equalled 0.0001 and was not significant, suggesting no population structure between Bonne Bay and GSL cod. Observed heterozygosity at *Pan* I locus was lower that for microsatellites. F_{IS} values

indicated no departure from Hardy-Weinberg equilibrium for both GSL and Bonne Bay cod. Similar to the microsatellites data, F_{ST} values for *Pan* I suggested no population structure (Table 4.4).

4.3.5. Population dynamics

Catches of Atlantic cod in Bonne Bay varied from 9 to 55 tons from 1996 to 2011, except for moratorium years (1994-1995 and 2003) during which landings were < 2 tons (Figure 4.9). Since 2009, catches have steadily decreased to reach a low level of 9 tons in 2011. Assuming a self-sustaining population of Atlantic cod in Bonne Bay with an initial biomass of 110 tons in 1994, the surplus production model showed that the biomass increased from 110 to 160 tons following the first moratorium (1994-96). The increase in catches after the 2003 moratorium resulted in the extinction of the population in 2005.

4.3.6. Comparison of age-0 juvenile cod abundance among sampling sites

The number of juvenile cod caught per tow of the 25 m beach seine was highly variable. Many tows caught no cod. A few tows caught dozens of cod. The total number of cod caught by the 25 m seine over the ten years of sampling in June month is 302, of which 273 were smaller than 96 mm SL. Averaged over all sites and all years, the 25 m beach seine collected 2.2 age-0 cod per tow. Because of the extreme variability within sites and years, the mean number of age-0 cod collected per tow of the 25 m beach seine did not differ significantly among sites, controlled for year (Table 4.5). Randomization test using 5000 iterations confirmed that the null hypothesis was not rejected. In the analysis of

trends (Table 4.6), there was no significant difference in trends across sites ($F_{4,117} = 1.88$, $p = 0.12$); nor was there any trend when all years were considered together ($F_{1,117} = 0.71$, $p = 0.4$).

4.4. Discussion

This study revealed that all size and age classes from age-0 juvenile to spawning adult cod are present in Bonne Bay. Although length frequency distribution partly reflected different sampling efforts from various gears, the fact that length frequency distribution were skewed towards juvenile size classes suggesting that East Arm Bonne Bay serves as a nursery area for juvenile cod, but the bay does not support an abundance of adult cod. Previous knowledge on juvenile cod distribution in the nGSL was limited to August bottom trawl research surveys, which indicated that age-1-4 cod were principally distributed along the slope of the Esquiman Channel and in Port-au-Choix area (Castonguay and Valois, 2007; Tamdrari et al., 2010). Data presented in this study expectedly extend the distribution of juvenile cod, especially age 0-1 cod, to inshore waters along the west coast of Newfoundland, but mainly raise questions about the natal origin of the juveniles present in Bonne Bay, and the degree of demographic dependency of Bonne Bay cod to the nGSL cod population.

Females in spawning condition were caught in South Arm Bonne Bay during the first two weeks of July 2009 and July 2010, indicating summer spawning in Bonne Bay. The proportion of females in spawning condition observed in this study (22%) was within the documented range of females in spawning condition observed in mid-June south of Bonne Bay (53% off Bay of Islands; Méthot et al., 2005) and in late July north of Bonne Bay (2% near the Strait of Belle-Isle; Méthot et al., 2005). Atlantic cod is a batch spawner and females release several batches of eggs for up to 50 days (Kjesbu, 1989). The spawning season in the nGSL traditionally starts end of March early April off St. George's Bay and continues while individuals migrate northward along the west coast of Newfoundland in June-July (Ouellet et al., 1997; Méthot et al., 2005). Spawning observed in Bonne Bay in this study thus does not appear temporarily isolated from spawning in the Gulf, but rather appears integrated into the protracted spawning season.

In eastern Newfoundland, juvenile Atlantic cod settle in shallow coastal waters at ~ 25-60 mm SL in several pulses from late August to mid-October (Methven and Bajdik, 1994). The presence of 26-42 mm SL juvenile cod in East Arm Bonne Bay in October indicated a fall settlement, concordant in time with spawning events observed in July in South Arm Bonne Bay. The small length-at-age of the juveniles caught in June in East Arm Bonne Bay (60-96 mm SL at one year old) was also consistent with summer spawning and fall settlement. The predominant north-eastward direction of summer wind stress in Bonne Bay (Figure 4.7) and the high coherence between wind stress and water velocity across the sill (Richards, 2005) suggest that advection of pelagic stages from

South Arm into East Arm Bonne Bay is plausible, despite the estuarine circulation. The mean cyclonic circulation in the Gulf and the shoreward Ekman transport along western Newfoundland resulting from prevailing south-westerly winds (Koutitonsky and Bugden, 1991) also suggest that pelagic juveniles may drift from the Gulf into Bonne Bay. Advection of juvenile cod from the Gulf into Bonne Bay may be facilitated by episodic winds that force surface flow into Bonne Bay and by the tendency of pelagic juvenile cod to move downward in the water column (Ings et al., 2008). Juvenile cod found into Bonne Bay may thus comprise a mixture of individuals spawned in the Gulf and individuals spawned into the Bay.

Genetic analysis using microsatellites and the *Pan* I locus revealed no genetic differentiation between cod from Bonne Bay and those from the nGSL, suggesting that no isolated population inhabits Bonne Bay. The *Pan* I locus has been successful in differentiating between resident and migratory cod in Norway and in Iceland (Sarvas and Fevolden, 2005; Pampoulie et al., 2008). Microsatellites have been successful in identifying small size populations confined in fjords in Norway (Jorde et al., 2007) and in Gilbert Bay (Ruzzante et al., 2000b), and even weak genetic differentiation has been detected using less than 11 microsatellites (Ruzzante et al., 2000a; Kovach et al., 2010). Absence of genetic structure is thus more likely to reflect gene flow rather than a lack of analytical sensitivity. In contrast to Gilbert Bay where prevailing winds do not favor immigration of pelagic stages into the fjord (Best et al., 2011), immigration rate of

pelagic stages from the Gulf into Bonne Bay may induce sufficient gene flow to prevent genetic differentiation due to local production.

The absence of genetic structure between Bonne Bay cod and nGSL cod further contrasts with the case of the Acadian redfish (*Sebastes fasciatus*). Similar genetic analyses performed on redfish from Bonne Bay and from the Gulf of St. Lawrence have revealed that a genetically distinct population of redfish occupies East Arm Bonne Bay (Valentin, 2006). Acadian redfish differ from Atlantic cod in their reproductive strategy. Atlantic cod display external fertilization of released eggs. Redfish display internal fertilization and ovoviviparity. Extrusion of live larvae reduces dispersal duration and distance, comparatively to eggs and larvae cod, and may consequently impede advection of redfish larvae within Bonne Bay. This reinforces the hypothesis of substantial advection of cod pelagic stages into Bonne Bay.

The Schaefer production model developed in this study suggests that Bonne Bay does not support an abundance of adult resident cod. Post-moratorium catch levels were too high to allow the persistence of a local population, and current catches must be ensured by immigration of adult cod from the Gulf during the feeding season. Landings in Bonne Bay since the first moratorium followed a similar trend to landings in the nGSL, with a drop in 1998 and a continuous decrease in the most recent years (Figure 2 in DFO, 2012), which highlight the high connectivity between Bonne Bay and Gulf cod. It is also interesting to note that the current fishing effort for Atlantic cod in Bonne Bay is

distributed in the outer basin, and no fishery for cod occurs in the inner basin (Arnault Le Bris, pers. obs.; local fishers, pers. comm. 2010). If Bonne Bay had once harboured a local population of Atlantic cod as suggested by historical observations (NRC, 1899) and studies of fishers ecological knowledge (Goose et al., 2003; Murray et al., 2008), it is likely that this population has been extirpated, and that remaining resident individuals are part of the Gulf cod population.

Finally, the general linear model testing for the effect of sampling site on age-0 cod abundance revealed that no habitat within East Arm Bonne Bay supported significantly greater abundances of age-0 cod. Instead, age-0 cod were associated with diverse habitat types including eelgrass meadows, various seaweeds species, pebbles, and cobbles. All these habitats were characterized by some level of complexity compared to the sparsely vegetated fine bottom substrate. On the east coast of Newfoundland, age-0 cod preferentially settle in eelgrass beds whose structural complexity offers protection against predators and enhances food availability (Gotceitas et al., 1997; Linehan et al., 2001; Renkawitz et al., 2011). Eelgrass patches of intermediate density have been suggested to provide the optimal trade-off between predation risk and foraging success (Thistle et al., 2010). On Georges Bank, juvenile cod preferentially settled on gravel deposits rather than sandy bottoms (Lough, 2010). While keeping in mind that habitat selection by age-0 cod varies across temporal and spatial scales (Methven and Bajdik, 1994; Schneider et al., 2008), and that the variance observed in age-0 cod abundance across sites and years was high, results of this study suggest that conservation efforts to

protect juvenile cod should not focus on any habitat types, but should aim at preserving the structural complexity of Bonne Bay nearshore habitats. At a scale of the Gulf of St. Lawrence, distribution and habitat association of age-0 cod remains completely mysterious and deserves increased attention.

4.5. Conclusion

In this study, several sources of information were combined to examine the abundance and distribution of adult and juvenile cod in the fjord of Bonne Bay and to investigate whether Bonne Bay harbours a local population of Atlantic cod. Nearshore water survey and fishery data revealed that Bonne Bay does not support an abundance of adult Atlantic cod, but that the bay provides a nursery area for juvenile cod. The presence of adults in spawning condition during the summer, the settlement of juveniles during the fall, and the length-at-age of 0+ cod indicated local recruitment into the bay. However, prevailing winds in the summer and the absence of genetic differentiation suggested that advection of cod pelagic stages from the Gulf represents a substantial source of recruitment. Further research on eggs and larvae distribution and on otolith composition would be useful to support these conclusions.

Although Bonne Bay supports neither a genetically unique population of Atlantic cod as in Gilbert Bay, nor a large aggregation as in Smith Sound Trinity Bay,

conservation efforts to preserve the diversity of habitats available for juvenile cod into the bay may help the rebuilding of the population. Recently, Bonne Bay has become a focus for stewardship efforts by coastal communities because the fjord-estuary ecosystem supports small boat fisheries, recreational fishing, pleasure boating, and ecotourism (Wroblewski, 2013). The documentation of Bonne Bay as a nursery and spawning area for cod may foster local stewardship, a pillar for the sustainable co-management of marine resources (Gutierrez et al., 2011).

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Tables

Table 4.1. Sampling effort at the seven collection sites within Bonne Bay: number of standardized tows with the 10 m beach seine, 25 m beach seine, and bottom trawl; number of standardized sets of gillnets. Site 1 could not be sampled with the 25m beach seine because of the presence of numerous boulders. Site 3A was too shallow to use the 25m beach seine and gillnets. Bottom-trawl could only be used on flat sandy bottom.

Sampling gear	Site	2002	2003	2004	2005	2006	2007	2008	2009	2009-Oct	2010	2011
10m beach seine	Site 1	2	10	10	19		3	2	2		2	3
	Site 2		12	11	7	27	4	6	3		11	8
	Site 2A							3	4			8
	Site 3	4	4	10	20	3	3	4	5		9	5
	Site 3A	2	2	15	5	3	3	5	2		2	3
	Site 4						3	3	7		3	7
	Site 4A						3	4	6		2	6
25m beach seine	Site 2		4	4	8	21	4	4	5	6	4	5
	Site 2A							3	3	6	1	2
	Site 3	4	1	2	5	3	3	4	5	6	5	3
	Site 4						2	3	4	6	3	4
	Site 4A						2	1	1		1	3
Gillnets	Site 1	5	1	13	7		3	3	4			
	Site 2		2	2	1	8	3	6	4		7	
	Site 2A							3	4		3	
	Site 3			3		2	4	6	10		4	
	Site 4						3	3	4			
	Site 4A						3					
Bottom trawl	Site 1	1										
	Site 3		2	11	1	4	4				3	
	Site 4A										1	

Table 4.2. Catch per unit of effort (number of cod / tow) using the 25m beach seine in East Arm Bonne Bay from 2002 to 2011.

CPUE	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	All years
Site 2		0	0.25	2.63	0	1.50	5.75	12.60	0.33	0	2.56
Site 2A							4.33	1.00	0	2	1.83
Site 3	1.75	0	0	0.40	1.33	1.00	1.75	0.40	2.20	0	0.88
Site 4						4.50	27.67	0.25	3.67	0.25	7.27
Site 4A						0	0	0	0	0	0.00
All sites	1.75	0	0.13	1.51	0.67	1.75	7.90	2.85	1.24	0.45	2.29

Table 4.3. Catch per unit of effort (number of cod / hour of immersion) using multi-panel and 3" mesh size gillnets in East Arm Bonne Bay from 2002 to 2010. No scientific license could be obtained for gillnets in 2011.

CPUE	2002	2003	2004	2005	2006	2007	2008	2009	2010	All years
Site 1	0.18	0.02	0.25	0.13		0.02	0.06	0.17		0.12
Site 2		0.02	0.50	0	0.04	3.00	0.68	0.30	0.03	0.57
Site 2A							0.22	0.06		0.14
Site 3			0		0.04			0.31	0.13	0.12
Site 4						0	0.04	0.06		0.04
Site 4A						0			0.04	0.02
All sites	0.18	0.02	0.25	0.07	0.04	0.76	0.25	0.18	0.06	0.24

Table 4.4. Genetic indices for microsatellites and *Pan* I locus on Atlantic cod from the Gulf of St. Lawrence (GSL) and Bonne Bay: observed (*Ho*) and expected (*He*) heterozygosities; F_{IS} and F_{ST} (significant departure from Hardy-Weinberg equilibrium are indicated with *, ns: non-significant); mean locus allelic richness (*Arich*); Allelic frequencies for *Pan* I locus (*Pan* I^A and *Pan* I^B). Sampling date, size (n), and mean fork length (FL) with standard deviation (SD) are indicated.

	Date	n	LF (SD)	*Ho*	*He*	F_{IS}	*Arich*	
Microsatellites								
Bonne Bay	2009	59	36.4 (6.7)	0.677	0.717	0.056 ns	10.1	ns
GSL	2002, 05, 07	139	56.0 (6.6)	0.65	0.698	0.070*	10.1	
Pan I							*Allele freq.*	
Bonne Bay	2009	55	36.3 (6.6)	0.418	0.409	0.000 ns	0.72 / 0.28	ns
GSL	2002, 05, 07	144	56.0 (6.6)	0.4444	0.467	0.048 ns	0.63 / 0.37	

F_{ST}	Microsatellites	*Pan* I
	0.0001 ns	0.010 ns

Table 4.5. Two-way ANOVA table for the effect of site (categorical) controlled for year (categorical) on the number of age-0 cod collected per tow of the 25 m beach seine. Five sampling sites (Site 2, 2A, 3, 4, 4A) and ten years of sampling during June from 2002 to 2011 were considered in the analysis. The value in brackets indicates new p-value obtained after randomization of the residuals.

Source	SS	df	MS	F	p-value
Year	316.89	9.00	35.21		
Site	124.69	4.00	31.17	1.61	0.18 (0.17)
Error	2184.84	113.00	19.33		
Total	2626.43	126.00			

Table 4.6. Two-way ANOVA table for the effect of site (categorical) and year (continuous) on the number of age-0 cod collected per tow of the 25 m beach seine. Five sites (Site 2, 2A, 3, 4, 4A) and ten years of sampling during June from 2002 to 2011 were considered in the analysis. The values in brackets indicate new p-values obtained after randomization of the residuals.

Source	SS	df	MS	F	p-value
Year	13.91	1.00	13.91	0.71	0.4 (0.4)
Site	147.68	4.00	36.92	1.88	0.12 (0.14)
Year * Site	162.55	4.00	40.64	2.07	0.09 (0.14)
Error	2302.29	117.00	19.68		
Total	2626.43	126.00			

Figures

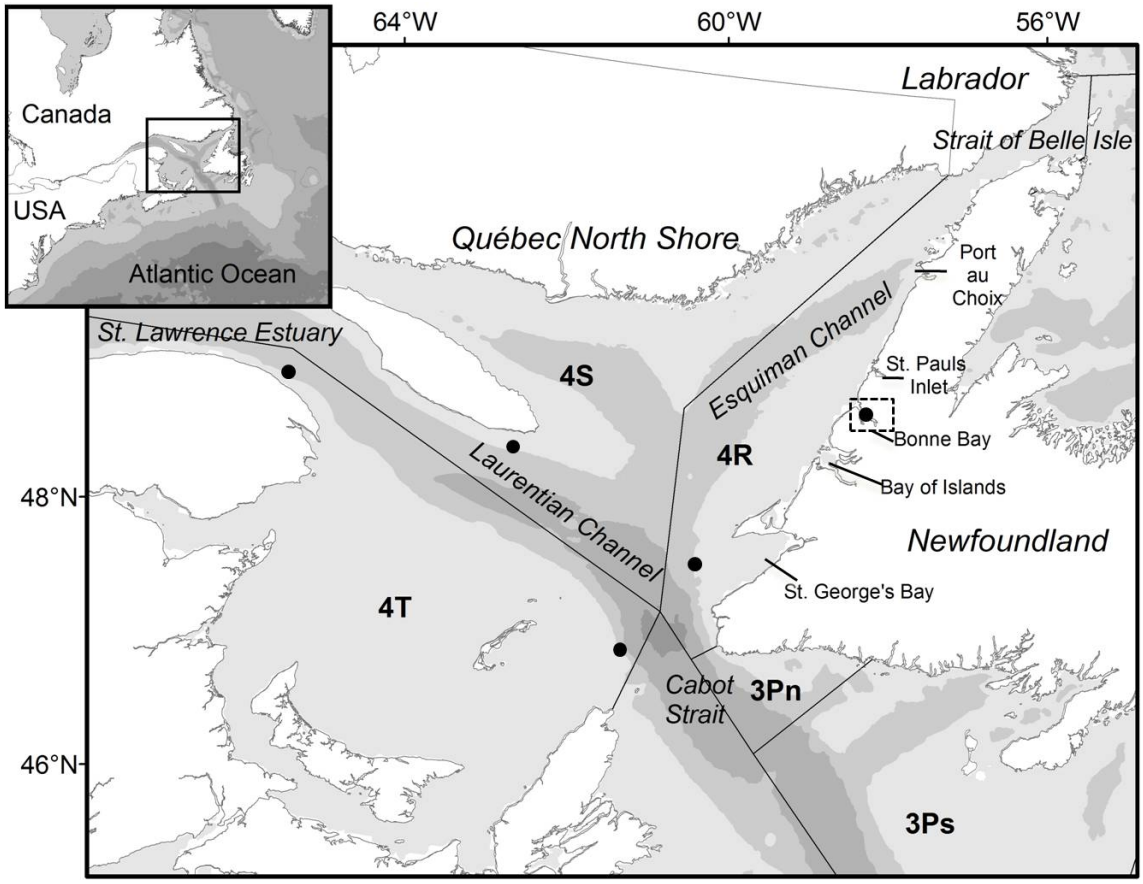

Figure 4.1. Map of the Gulf of St. Lawrence with the location of Bonne Bay. Black circles show sampling locations of Atlantic cod used for genetic analysis. Black lines delimit the NAFO management divisions. The grey contours on the main map represent the 200, 400, 500 meter isobaths.

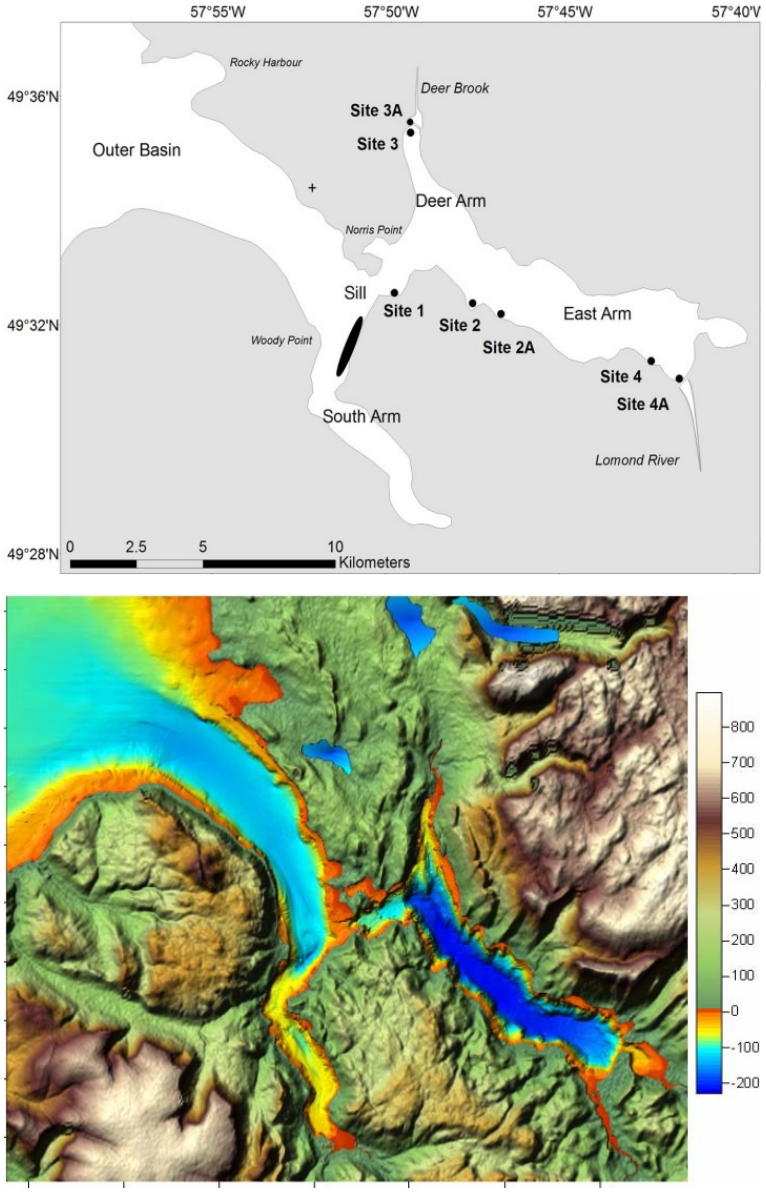

Figure 4.2. Maps of Bonne Bay. Top: map of Bonne Bay showing sampling sites (black circles) and the location of sampling with commercial fishermen (black oval). Black cross shows location of weather station. Bottom: bathymetry and topography of the Bonne Bay region (from Richards, 2005). Depth is in meters.

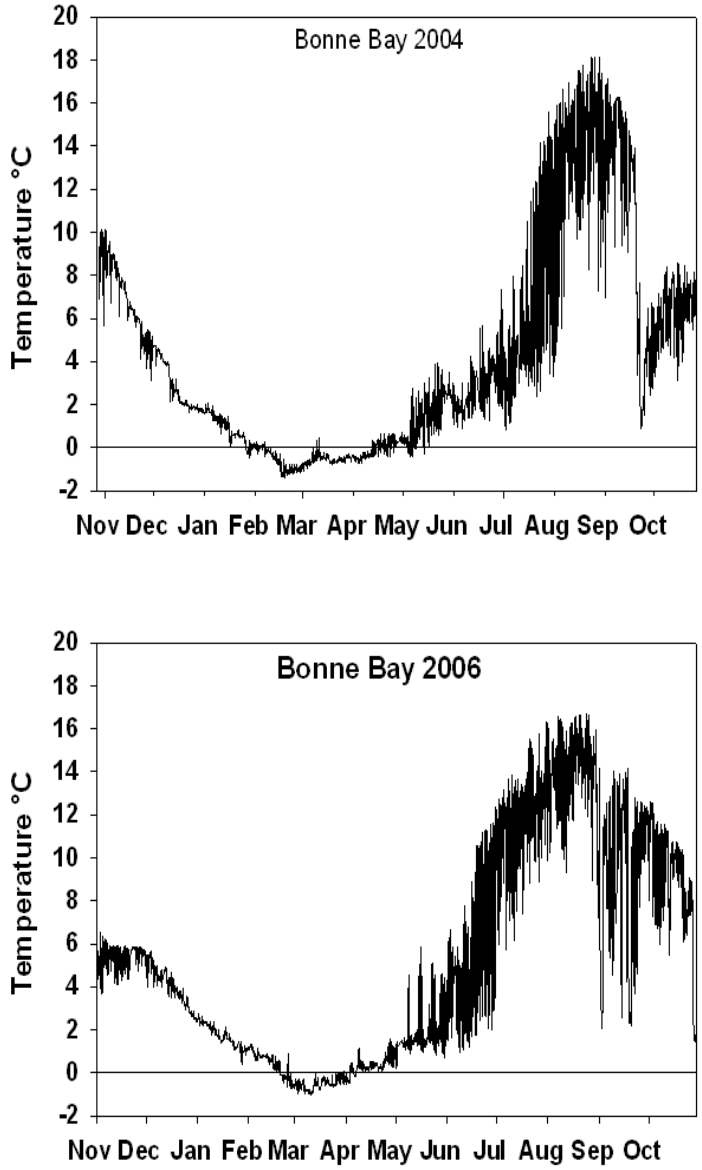

Figure 4.3. Water temperatures recorded in Bonne Bay above the inner sill at depth of 18 meters.

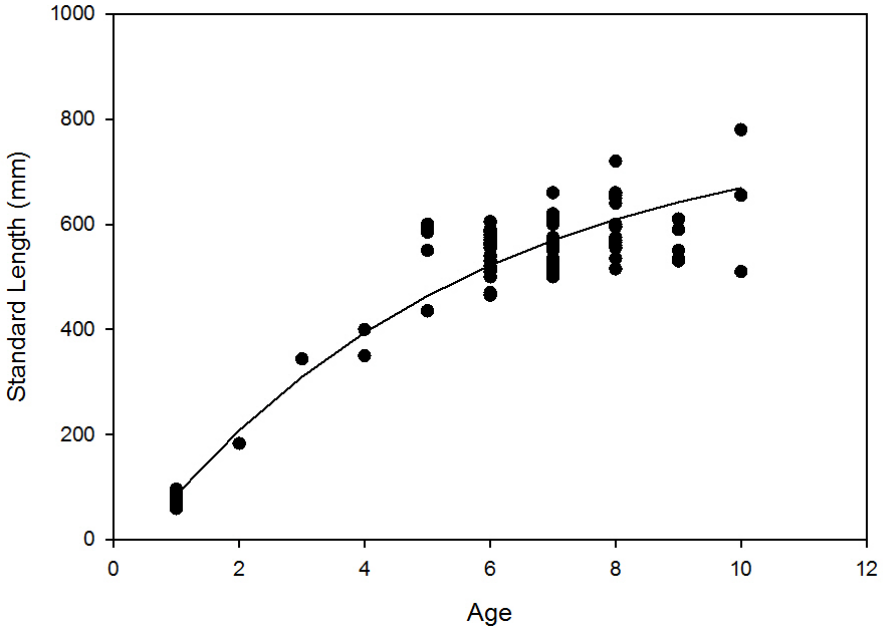

Figure 4.4. von Bertalanffy growth curve fitted with a non-linear least square approach. Black dots show length-at-age observations from otolith readings (n = 100). $f(x) = 800 \times \left(1 - e^{-0.19 \times (x-0.4)}\right)$. $r^2 = 0.93$.

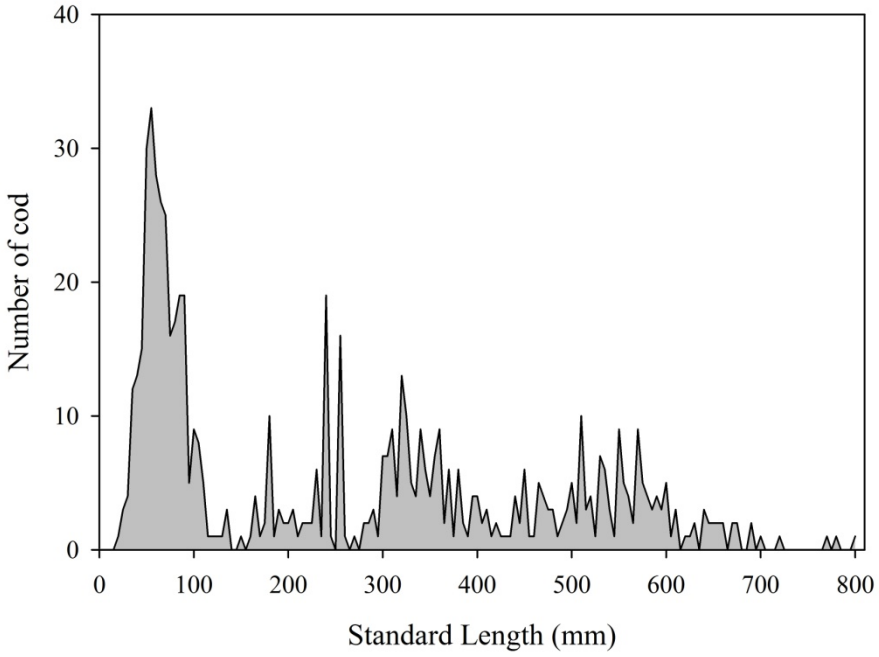

Figure 4.5. Length frequency distribution of Atlantic cod collected in Bonne Bay using all gear types during the ten years of sampling from 2002 to 2011. Measured standard lengths were binned into 5 mm intervals. n = 676.

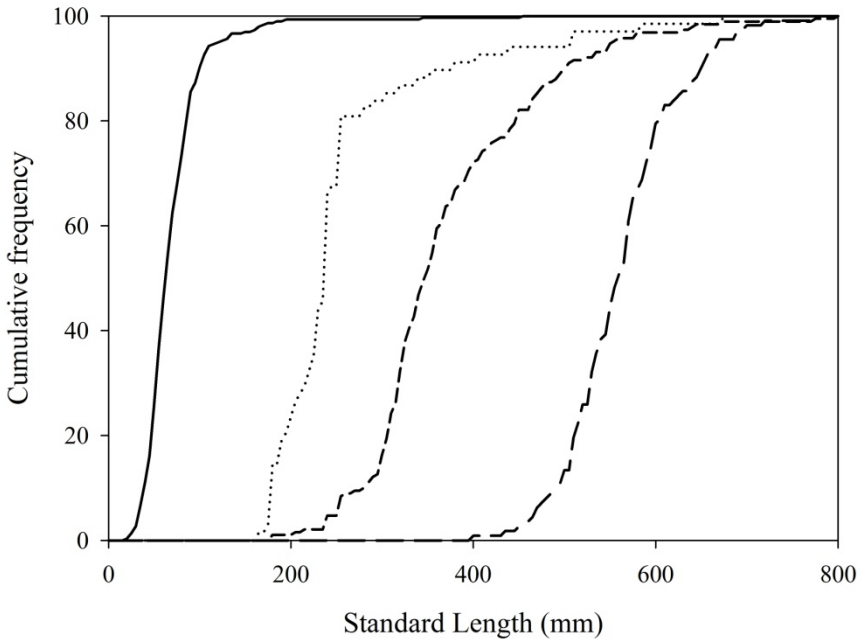

Figure 4.6. Selectivity of the multiple gears used to sample cod in Bonne Bay. Solid line: 25m beach seine. Dotted line: multi-panels gillnet (1", 1.5", and 2" mesh size panels). Short-dashed line: 3" mesh size gillnet. Long-dashed line: 6" mesh-size commercial gillnet.

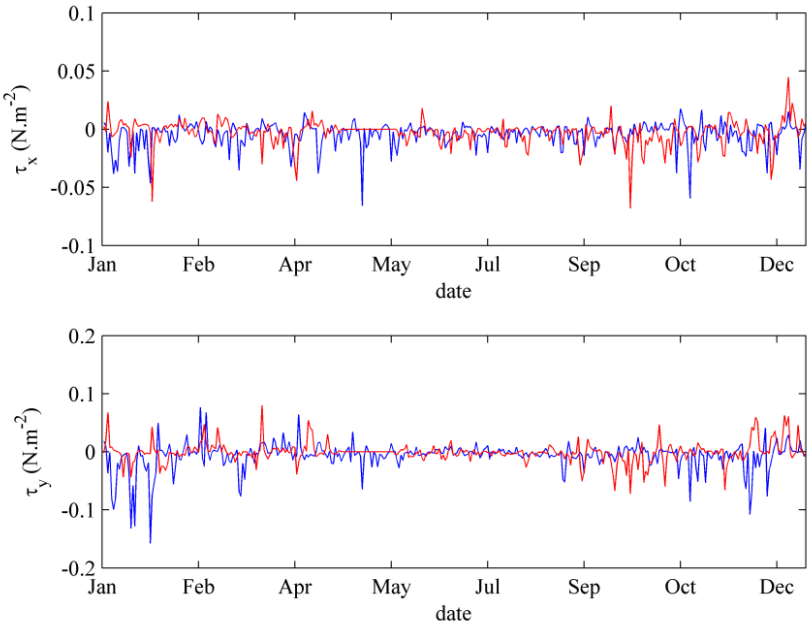

Figure 4.7. Daily mean wind stress. Postive τ_x indicates wind stress towards the West. Postive τ_y indicates wind stress towards the South. Blue line = 2009 data. Red line = 2010 data.

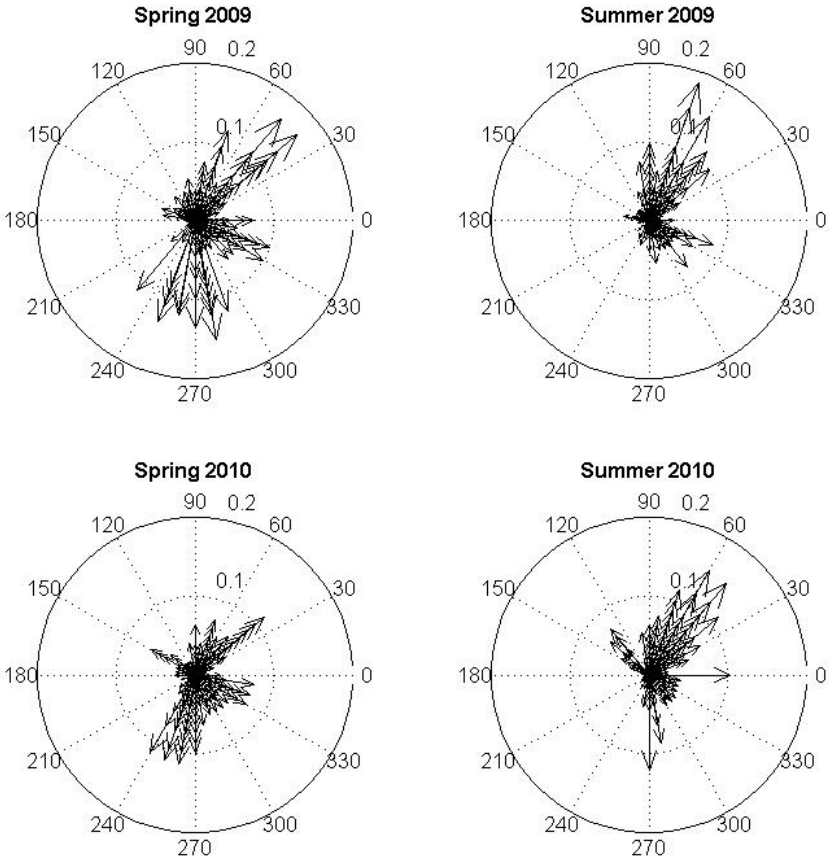

Figure 4.8. Spring and summer 2009 and 2010 wind stresses. Wind stress direction follows oceanographic convention (arrows point destination).

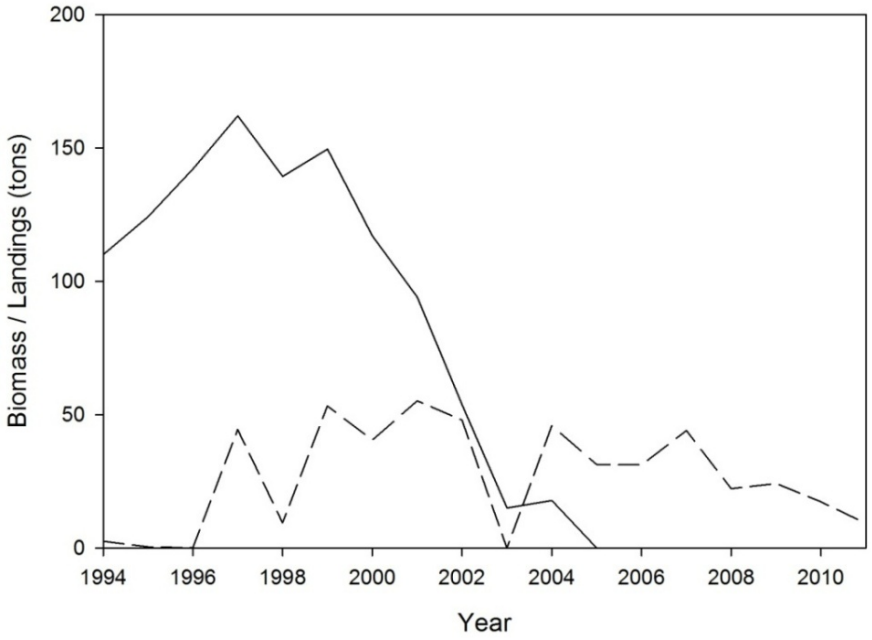

Figure 4.9. Landings (dashed line) and estimated biomass (solid line) using a Schaefer model for Atlantic cod in Bonne Bay from 1994 to 2011. Years 1994, 1995, 1996, and 2003 are moratorium years. Parameter values used in the Schaeffer model are: K = 550 tons, r = 0.19 $year^{-1}$, initial biomass = 110 tons (20% of K).

Chapter 5. Supplementing Electronic Tagging with Conventional Tagging to Redesign Fishery Closed Areas

Arnault Le Bris[1*], Alain Fréchet[2], Joseph S. Wroblewski[3]

[1]Biology Department, Memorial University of Newfoundland, St. John's, NL, Canada

[2]Maurice-Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, QC, Canada

[3]Department of Ocean Sciences, Memorial University of Newfoundland, NL, Canada

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Abstract

Fishery closed areas provide a resource management tool to protect predictable spawning aggregations of migratory fish species. Movement by individual fish however challenges the effectiveness of fishery closed areas. Recent developments in electronic tags and movement modeling offer new information to quantify fine-scale usage of fishery closed areas by free-ranging individuals. Conventional tagging data, on the other hand, provide population broad-scale distribution patterns with respect to closed areas. Using the Atlantic cod (*Gadus morhua*) population from the northern Gulf of St. Lawrence as a case study, we demonstrate how electronic tagging experiments can be supplemented with conventional tagging experiments to evaluate and redesign fishery closed areas. A geolocation model was used to estimate time of arrival, time of departure, and proportion of time that individual cod equipped with data-storage tags spent within a fishery closed area. Two heurisitc algorithms were developed to seek out the spatial and temporal designs that maximized the proportion of time that the fish equipped with data-storage tags spent inside the closed area, relative to its size and duration. Bootstrap analyses quantified the effects of inter-individual variability in closed area usages. Conventional tagging data were used to estimate the proportion of the spawning population density function encompassed by the closed area. Results from the electronic and conventional tagging experiments suggested that the fishery closed area in the northern Gulf of St. Lawrence should be displaced south along the 200-m isobath and that the enforcement period be reduced. Electronic tagging data also suggested that alternative migratory

behaviours within a population lead to disproportional levels of protection between migratory and non-migratory groups. A re-examination of past conventional tagging experiments in combination with recent electronic tagging experiments provides new information to evaluate the spatiotemporal design of fishery closed areas.

5.1. Introduction

The tendency of commercial fish species to aggregate during predictable spawning periods exacerbates their vulnerability to human exploitation. Fishery closed areas on migratory corridors and spawning grounds provide a resource management tool to help rebuild depleted populations (Murawski et al., 2000; Jensen et al., 2010). Fishery closed areas on spawning grounds have limited benefits if constant catch levels are applied outside closed areas (Horwood et al., 1998; Walters et al., 2007; West et al., 2009; Grüss et al., 2013). However, when appropriately designed and combined with other management measures that control for fishing effort in adjacent areas, fishery closed areas on spawning grounds may help rebuild a depleted migratory population by reducing mortality rates on the spawning stock biomass, and avoiding disruption of the reproductive activity (Beets and Friedlander, 1999; Rowe and Hutchings, 2003; Stefansson and Rosenberg, 2006). Although the level of protection afforded by a fishery closed area partly depends upon adult movements across closed area boundaries, and upon size of population distributional range relative to closed area size (Murawski et al.,

2000; O'Boyle, 2011), adult movements and population distribution with respect to closed areas remain recurrent knowledge gaps to closed areas design and implementation (Sale et al., 2005; Grüss et al., 2011a).

Recent advances in electronic fish tracking technologies and concurrent developments in the modelling of tracking data have revolutionized the study of animal movement (Nathan et al., 2008). Migration routes of numerous marine migratory species are now being reconstructed (Block et al., 2011), including pelagic (Block et al., 2005; Kraus et al., 2011) and demersal migratory fish species (Svedäng et al., 2007; Mitamura et al., 2009). When direct observations of fish positions are not available from the tag, fish positions are inferred from the recorded environmental variables using robust and widely available statistical geolocation models (Patterson et al., 2008; Evans and Arnold, 2009; Jonsen et al., 2013). Probability distribution functions of fish position resulting from geolocation models allow the quantification of fine-scale usage of closed areas by free-ranging adult fish (Andersen et al., 2007). As such, electronic tagging (ET) experiments offer unprecedented opportunities to refine the spatiotemporal design of fishery closed areas from fishery independent observations. It should be noted that electronic tagging experiment depends on the fishery or scientific surveys to capture the fish, and in the case of data-storage tags, to recapture the fish. As such electronic tags are not fully independent from the fishery. If the fishery tend to capture more one specific behaviour (e.g. migrant instead of resident), then the sample of tagged fish may be biased toward that specific behaviour.

The cost of fish tracking devices limits the number of tagged individuals in practice. Although conventional tagging (CT) data are fishery dependent and have limited temporal resolution, the larger number of tagged fish facilitates inferences to the population for broad-scale patterns (Bolle et al., 2005; Espeland et al., 2008). Recapture locations from CT experiments can be used to estimate the tagged population density function over determined periods (Righton et al., 2007; Espeland et al., 2008). Recently, combinations of ET and CT experiments have been used to study seasonal migration across management division boundaries and to estimate stock exploitation rates (Righton et al., 2007; Kurota et al., 2009). In this study, we demonstrate that combination of ET and CT experiments can also be used to evaluate and redesign fishery closed areas. Indeed, the fine spatial and temporal scale observations gathered from ET experiments, and the broad-scale spatial observations gathered from CT experiments, provide different yet complementary datasets to quantify, first, the extent of movement across closed areas boundaries, and second, the proportion of the spawning population density function encompassed by closed areas.

This study demonstrates how ET experiments can be supplemented with CT experiments to redesign fishery closed areas. A fishery closed area designed to protect a spawning aggregation of Atlantic cod (*Gadus morhua*) in the northern Gulf of St. Lawrence is the case study presented here. A geolocation model was used to estimate the proportion of time that Atlantic cod equipped with data-storage tags (DSTs) spent inside the closed area during the enforcement period. A spatial heuristic algorithm and a

temporal heuristic algorithm were developed to refine the closed area design. Bootstrap analyses quantified the effects of inter-individual variability in closed area usages on the estimated proportion of time spent within the closed area. Kernel density estimations of recapture positions from three CT experiment programs (two pre-population collapse 1983-1985 programs and one post-population collapse 1995-2002 program), were used to estimate the proportion of the tagged population density function encompassed by the closed area. Encompassed proportions were estimated for four closed area designs identified beforehand with the two heuristic algorithms.

The Atlantic cod population from the northern Gulf of St. Lawrence (nGSL, Figure 5.1) collapsed in the late 1980s and early 1990s (Fréchet et al., 2009). Despite two moratoria on the fishery, a first one from 1994 to 1996 and a second one in 2003, a two decade long drastic reduction in the fishing effort, and a ban of commercial trawling for groundfish in the nGSL since 1997, the population went from a “threatened” status in 2003 (COSEWIC, 2003) to a more severe “endangered” status in 2010 (COSEWIC, 2010). The bulk of the population overwinters in the relatively deep water of the Laurentian Channel (Campana et al., 1999). In early spring, cod start migrating towards the main spawning ground located off the southwest coast of Newfoundland, off St. George's Bay (Ouellet et al., 1997; Méthot et al., 2005). In late spring, cod leave the main spawning ground to reach summer feeding grounds along the Newfoundland west coast and the Québec North Shore (Yvelin et al., 2005). The documentation of a remaining spawning aggregation of Atlantic cod by combined acoustic, ichthyoplankton, and

bottom-trawl surveys conducted in the springs 1993, 1994, 1995, and 1998 (Ouellet et al., 1997; McQuinn et al., 2005) led to the implementation of a seasonal fishery closed area in 2002 (FRCC, 2002; DFO, 2003). The closed area approximates 5000 km^2 and is delimited by the following coordinates: 48°15'N - 49°10'N and 59°20'W - 60°00'W (Figure5.1). The fishery closure prohibits all ground fishing activities yearly from April 1st to June 15th, in order to reduce adult mortality rate, avoid disruption of the reproductive activity, and prevent bycatch of Atlantic cod in other demersal fisheries, including redfish (*Sebastes* spp.), Atlantic halibut (*Hippoglossus hippoglossus*), witch flounder (*Glyptocephalus cynoglossus*), turbot (*Reinhardtius hippoglossoides*). However, in the absence of surveys and catch data during the enforcement period, no attempt has been made to evaluate and redesign the fishery closed area since its implementation in 2002.

5.2. Material and Methods

5.2.1. Electronic tagging

An ET experiment program using DSTs was conducted in the nGSL from 2007 to 2012. A total of 353 Atlantic cod (fork length >40 cm) were captured using baited handlines and surgically implanted with DSTs inside the abdominal cavity. Tagging locations were chosen to cover the three Northwest Atlantic Fisheries Organization (NAFO) management units in the nGSL (NAFO divisions 3Pn, 4R, and 4S, Figure 5.1). DSTs

recorded temperature and pressure over time. Lotek tag series LTD_1100 and LAT_1400 (Lotek Wireless Inc., www.lotek.com) were used in the experiments (Appendix D). T-bar anchor tags were fixed in the dorsal musculature to alert harvesters about the presence of the internal tag. Advertisement and reward campaigns were used to increase tag reporting rate. Data were successfully downloaded from 17 recovered DSTs. Time series with incomplete record during the April 1st - June 15th period were removed. A total of 14 DSTs were used in this study (Table 5.1).

5.2.2. Geolocation

A geolocation model was used to reconstruct migration routes of Atlantic cod equipped with DSTs in the nGSL (Le Bris et al., 2013a). The low tidal range in the Gulf of St. Lawrence prevented the use of the tidal location method to infer fish position (Metcalfe and Arnold, 1997; Hunter et al., 2003a). The model instead compared the daily maximum depth (*i.e.* deepest depth) and the associated temperature recorded by the tag, with depth and temperature from bathymetric and seasonal bottom temperature grids (Galbraith et al., 2012). The model relied on a hidden Markov model (HMM) to compute the posterior probability distribution function of fish daily location (Pedersen et al., 2008; Thygesen et al., 2009). HMMs consist in two coupled stochastic models: the process model and the observation model. For each tracked day, the process model simulated individual fish movement in the plane using a diffusion equation:

$$\frac{\partial \varphi(\boldsymbol{x},t)}{\partial t} = D\left[\frac{\partial^2 \varphi(\boldsymbol{x},t)}{\partial x^2} + \frac{\partial^2 \varphi(\boldsymbol{x},t)}{\partial y^2}\right] \qquad (5.1)$$

where $\varphi(\boldsymbol{x}, t)$ is the probability distribution function of the fish position (*i.e.* the probability that the fish is located at position $\boldsymbol{x}(x, y)$ at time $t = \{1, \dots, T\}$), and D represents the diffusion rate. This partial differential equation was discretized in space onto a 2 km resolution grid (331×476 regular grid cells) and time (number of recording days T) and solved using finite differences.

The observation model refined positions predicted by the movement model by assigning a likelihood value based on the match between bathymetry and bottom temperature at the estimated position $\boldsymbol{x}(x, y)$ and the daily maximum depth and associated temperature recorded by the tag $\boldsymbol{y}(z, tp)$. Atlantic cod is a demersal fish species. It was assumed that Atlantic cod in the nGSL visit the seafloor at least once a day. Daily maximum depth recorded by the tag and the associated temperature were thus considered representative of the sea floor and of the bottom temperature. In absence of information on the distribution of the bathymetry and bottom temperature errors for a given grid cell, errors were assumed to follow a normal distribution. In order to consider errors arising from tag measurements (accuracy of ±1% and ±0.2°C for pressure and temperature sensors, respectively), the observational likelihood (*i.e.* likelihood of observations $\boldsymbol{y}$ given position $\boldsymbol{x}$) was evaluated between depth interval [z_1 z_2] and temperature interval [tp_1 tp_2] rather than at fixed values. Intervals [z_1 z_2] and [tp_1 tp_2] were defined by $z_1 = z*0.99$, $z_2 = z*1.01$, $tp_1 = tp-0.2$, $tp_2 = tp+0.2$, where z is daily maximum depth recorded by the tag, and tp is the temperature recorded by the tag at the daily maximum depth. Depth and bottom temperature were assumed as independent. The

likelihood of a location given the observed maximum depth and associated temperature was thus obtained by the product of two normal distribution functions integrated inside the previously defined intervals:

$$L(\boldsymbol{x}) = \int_{z_1}^{z_2} N(z; \mu_z, \sigma_z) dz * \int_{tp_1}^{tp_2} N\big(tp; \mu_{tp}, \sigma_{tpz}\big) dtp \quad (5.2)$$

where $N(w; \mu, \sigma)$ is a normal probability distribution function of mean μ and standard deviation σ, μ_z the grid cell bathymetry, σ_z the grid cell bathymetry standard deviation, μ_{tp} the grid cell bottom temperature, and σ_{tp} is the grid cell bottom temperature standard deviation.

Standard deviation of a grid cell bathymetry was estimated prior to the geolocation model using bathymetry from the eight adjacent grid cells:

$$\sigma_z = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(z_i - \bar{z})} \quad (5.3)$$

where z_i is the bathymetry of the adjacent cell i with n = 8, and $\bar{z}$ is the mean bathymetry of the eight adjacent cells. The same approach was used to estimate the standard deviation of grid cell bottom temperature. High bathymetry and bottom temperature standard deviations are found in areas of marked topographic changes (*i.e.* along the slope of the channels and in coastal areas) and result in wider probability distribution functions of daily fish location.

Within the HMM framework, the finite and discrete nature of the state (*i.e.* fish location in this study) allows the use of a maximum likelihood approach to estimate model parameters (Cappé et al., 2005). The parameter *D* was estimated by minimizing the negative log likelihood function:

$$L(D) = -\sum_{t=1}^{T} \log \lambda_t \quad (5.4)$$

where λ_t is the normalizing constant obtained from predictions of individual daily location. The numerical optimizer *fminbnd* in Matlab R2012a (The Mathworks, Natick, MA) was used to minimize the negative log-likelihood function. Finally, a smoothing filter was used to refine estimations of fish positions by computing the full posterior distribution conditional on all observations. Detailed explanations of the maximum likelihood approach and the smoothing filter are provided in Thygesen et al. (2009).

Daily probability distribution functions resulting from the geolocation model can be used to estimate the proportion of time that an individual spent inside an area over a determined period (Pedersen et al., 2011). Similarly, the average time that a group of tagged individuals spent inside an area can be estimated by averaging individual daily probability distribution functions (Andersen et al., 2007). The proportion of time that the group of fish equipped with DSTs spent inside the closed area during its enforcement period (April 1st – June 15th) was calculated as follows:

$$p(\boldsymbol{x}) = \frac{1}{n}\frac{1}{\mathrm{T}}\sum_{i=1}^{n}\sum_{1}^{T}\sum_{\boldsymbol{x_{ins}}} \varphi_i(\boldsymbol{x}_{ins}, t) \quad (5.5)$$

where $\varphi_i(\boldsymbol{x}_{ins}, t)$ is the probability that individual i was located at position $\boldsymbol{x}_{ins}(x, y)$ inside the closed area at day t, T the time interval of the enforcement period, and n is the total number of individual used in the study (n = 14).

5.2.3. Heuristic algorithms

Size and location are critical factors that affect the performance of fishery closed areas. Large areas have potentially greater protective benefits but may also have greater socio-economic costs associated with closed area enforcement and short-term reduction in catch per unit of effort (FAO, 2011). In order to seek out the closed area size and location that afford the maximum protection to the group of tagged fish while taking into account the size of the area, a spatial performance index was defined as follows:

$$SPI = \frac{p(\boldsymbol{x})}{\sqrt{S}} \tag{5.6}$$

where SPI is the spatial performance index, S is the surface area in km^2, and $p(\boldsymbol{x})$is the time proportion obtained in equation 5.5. The square root function was necessary to limit the influence of the denominator term. The highest performance index would otherwise always be obtained with the smallest area.

Once the spatial performance index was defined, the boundaries of the closed area were progressively displaced. Starting from the center point of the closed area (i.e. 48°30'S - 59°48'W), the closed area size was increased minute by minute in all the four

cardinal directions, successively. The following coordinates were used to bind the maximal size of the closed area: 47°30'N, 49°30'N, 59°W, and 60°30'W for the south, north, east, and west boundaries, respectively. After each modification to the closed area spatial design, the spatial performance index was calculated. The combination of north, south, east and west boundaries that yielded to the maximum value for the spatial performance index was considered as the optimal spatial design.

The time span of the enforcement period is another factor that affects the performance of temporary fishery closures. Similar to the spatial performance index, a temporal performance index was defined as follows:

$$TPI = \frac{p(\boldsymbol{x})}{\sqrt{T}} \tag{5.7}$$

where TPI is the temporal performance index $T$is the time interval of the enforcement period in days. Once again, the square root function in the denominator term was necessary to prevent the temporal performance index from identifying the single day with the highest proportion inside the closed area as the optimal temporal design. In order to find the enforcement period that afforded the maximum protection to the tagged group of cod relative to the number of enforced days, the $d(d-1)/2$ possible combinations of start and end dates between March 15th and June 30th (d = 108) were tested. For each time interval, the temporal performance index was estimated. The time interval that

yielded to the maximum value for the temporal performance index was considered as the optimal temporal design.

It is important to note that spatial and temporal designs were evaluated independently to limit the number of possible combinations in the heuristic algorithms. Indeed, 4.2×10^{10} combinations were possible if spatial and temporal designs were evaluated simultaneously, 7.3×10^{6} when only the spatial design was evaluated, and 5778 when only the temporal design was evaluated. This helped to reduce greatly computation times (heuristic algorithms were programmed in Matlab R2012a). Because spatial and temporal designs were evaluated using two independent algorithms, four scenarios of closed area design could be defined: i) original area and enforcement period, ii) optimal area and original enforcement period, iii) original area and optimal enforcement period, iv) optimal area and enforcement period. For each scenario, the average proportion of time that the entire group of tagged cod (n = 14), the group of migratory cod (n = 11), and the group of resident cod (n = 3) spent inside the closed area was estimated.

5.2.4. Bootstrap analyses

Inter-individual variability may induce bias in the quantification of fishery closed area usage by electronically tagged fish, especially when the number of recovered tags is low. Three bootstrap analyses were performed to quantify the sensitivity of the method to inter-individual variability in closed area usage. The first analysis quantified the effects of

the low number of recovered tags on the average proportion of time that the group of tagged fish spent inside the four closed area designs defined above. A random sampling with replacement of 7, 14 and 21 individuals from the initial pool of 14 fish equipped with DSTs was iterated 1000 times. At each iteration, the average proportions of time that the samples of 7, 14, and 21 individuals spent inside the four closed area designs were estimated and saved. Resulting probability densities were drawn using Matlab *ksdensity* function.

The second bootstrap analysis quantified the effects of inter-individual variability on the optimal spatial closure design. 14 individuals were randomly selected with replacement from the pool of 14 fish equipped with DSTs. The operation was iterated 100 times. 100 iterations were performed rather than 1000 so as to limit computation time. For each sample of 14 fish, the spatial heuristic algorithm was run. The south, north, east, and west closed area boundaries that maximized the spatial performance index were saved at each iteration. The mean and standard deviation of each boundary were then estimated, providing the average optimal spatial design and the associated uncertainty.

The third bootstrap analysis quantified the effects of inter-individual variability on the optimal temporal closure design. In this analysis, the random selection with replacement of 14 fish was iterated 1000 times. For each sample of 14 fish, the temporal heuristic algorithm was run and the combination of start and end dates that maximized the temporal performance index were saved. The mean and standard deviation of start and

end dates were then estimated, providing the average optimal enforcement period and the associated uncertainty.

5.2.5. Conventional tagging

Conventional tagging data originated from three tagging programs. Two programs were carried out during a historical period of high population abundance, and one was carried out during a recent period of low population abundance. The first program was directed by the Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ). About 15,000 Atlantic cod were tagged and released from 1983 to 1985 along the Québec North Shore (Figure 5.1). The second program was directed by the Department of Fisheries and Oceans Canada (DFO). A total of 28,919 Atlantic cod were tagged and released from 1983 to 1985 along the Québec North Shore and along the west coast of Newfoundland (Figure 5.1). The third program was part of the Gulf Sentinel Fishery Program. A total of 81,227 Atlantic cod were tagged and released from 1995 to 2012 throughout the nGSL. All CT experiments used T-bar anchor tags, which were inserted at the base of the first dorsal fin. Additional details on fish capture and tagging techniques can be found in Gascon et al. (1990) for the 1983-85 CT programs and in Bérubé and Fréchet (2001) for the 1995-2012 CT program.

Recapture positions from April 1st to June 15th prior to the closed area establishment in 2002 were used in the analysis. Recapture data with missing or improbable information (*e.g.* recapture position on land, no recapture date) were

removed. Fish recaptured outside NAFO divisions 3Pn and 4RS were also removed because they might belong to other populations. Finally, fish tagged and recaptured near Anticosti Island (Figure 5.1) were removed from the analysis and this for two reasons. First, no tagging and no recapture occurred in the Anticosti Island area for the post-collapse CT and ET experiments. Second, fish from the Anticosti Island area are thought to represent a sub-population of the nGSL cod population with a distinct spawning ground from the one studied here (Bui et al., 2011).

The two databases (MAPAQ and DFO) had 1659 and 3289 recaptures, of which 257 and 208 fulfilled the above selection criteria. The two databases were combined for a total of 465 recaptures for the pre-collapse period. The post-collapse Sentinel Program database had 6700 recaptures, of which 345 fulfilled the above selection criteria.

5.2.6. Kernel density estimation

Kernel methods allow efficient non-parametric estimation of density function from non-normally and multi-modally distributed observations (Worton, 1989; Seaman and Powell, 1996). Matlab *kde2d* function (Botev et al., 2010) was used to estimate the tagged population density during the fishery closure enforcement period from the pre- and post-collapse recapture positions. The function uses a bivariate Gaussian kernel density estimator based on a linear diffusion process. The tagged population density at the position $\boldsymbol{x}(x, y)$ was given by:

$$f(\boldsymbol{x}, \boldsymbol{h}) = \frac{1}{n\boldsymbol{h}} \sum_{i=1}^{n} K \frac{(\boldsymbol{x}-\boldsymbol{x}_i)}{\boldsymbol{h}} \quad (5.8)$$

where $\boldsymbol{h}$ is the anisotropic bandwidth parameter, n the number of tag recoveries, $\boldsymbol{x}_i$ the vector of longitude and latitude coordinates for recapture event i, and K is the bivariate Gaussian kernel. The bandwidth parameter was chosen optimally using a plug-in bandwidth selection method (see Botev et al., 2010 for more details). This method did not assume a preliminary parametric model for the data. It was therefore well suited to handle multimodal distributions with widely separated modes (values at which probability distribution is the highest) characteristic of conventional tagging data.

For the pre- and post-collapse CT programs, the proportion of the tagged population density function encompassed by the closed area was calculated using the four scenarios of closed area design identified in the electronic experiment. For the two scenarios in which the enforcement period was changed (scenarios 3 and 4), kernel densities were re-computed using recapture data corresponding to the new enforcement period.

Intrinsic bias in CT experiments may affect kernel density estimations. First, tag loss and tag reporting rates may vary in space and time (Cadigan and Brattey, 2003). Tag loss and reporting rates were assumed constant throughout the study period and area. Second, recapture locations often depict more the spatial distribution of the fishing effort rather than the true distribution of the tagged population (Bolle et al., 2005). It is

necessary to adjust tag recapture information by fishing effort. In the absence of detailed information on fishing effort, catch data per management unit were used to standardize kernel density estimations (Lawson and Rose, 2000; Schopka et al., 2010; Tamdrari et al., 2012b). Finally, group cohesion in Atlantic cod (Tamdrari et al., 2012a) may violate the assumption of independent observations. Adequate sample size (>50 observations) reduces bias in kernel density estimation induced by non-independent observations (Swihart and Slade, 1997; Seaman et al., 1999). Standardization of recaptures by catch data per unit area likely reduces this bias as well.

5.3. Results

5.3.1. Electronic tagging experiment

The spring probability distribution function for the group of Atlantic cod equipped with DSTs showed a multimodal distribution with three principal modes (Figure 5.2a). The first mode was located inside the original closed area along the 200-m isobath. The second mode was located south of the first mode following the 200-m isobath, near the tip of the southwest coast of Newfoundland. The third mode was located in nearshore waters along the west coast of Newfoundland. This third mode mainly corresponded to the distribution of non-migratory cod (Le Bris et al., 2013a). The distribution contour lines located along the slopes of the Esquiman Channel corresponded to individuals that left

the spring spawning area in late May and migrated towards their summer feeding grounds near the Strait of Belle Isle.

Tagged individuals spent on average 28.8% of their time inside the original fishery closed area from April 1st to June 15th. Daily analysis showed that the time spent inside the area increased from 4.8% on March 20th to 28.3% on April 1st, was maximal from mid-April to mid-May (~40%), and suddenly decreased from 27.1% on May 23rd to 9.8% on May 31st (Figure 5.3a). Separate analyses for the two behaviours revealed that migratory cod spent on average 36.6% of their time inside the original closed area, while non-migratory cod did not visit the closed area (Table 5.2).

5.3.2. Closed area optimal designs

The first heuristic algorithm searching for the optimal spatial design of the closed area revealed that the highest value for the spatial performance index was obtained with a 4770 km^2 area delimited by the following coordinates: 47°50'N - 48°44'N, 59°25'W - 60°04'W (Figure 5.2a). The proportion of time spent by the group of tagged fish inside this newly designed area was significantly higher than the proportion time spent inside the original area (Table 5.2, 38.2%, paired samples *t*-test, $t_{1,13} = 2.317$, $p = 0.04$).

The second heuristic algorithm searching for the optimal temporal design of the closed area revealed that the highest value for the temporal performance index was obtained with a shift of the enforcement period from April 1st - June 15th to March 27th - May 28th (Figure 5.3a). The proportion of time spent inside the closed area by the group

of tagged fish during the new enforcement period was significantly higher than during the original enforcement period (Table 5.2, 35.9%, paired samples *t*-test, $t_{1,13} = 3.663$, $p = 0.003$). The highest proportion of time spent inside the closed area was obtained when both spatial and temporal changes to the closed area were considered. This proportion was significantly higher than for the original spatial and temporal designs (Table 5.2, 50.3%, paired samples *t*-test, $t_{1,13} = 3.018$, $p = 0.01$).

5.3.3. Sensitivity to sample size and inter-individual variability

A bootstrap analysis was performed to quantify the effects of inter-individual variability on the proportion of time spent inside the closed area. For the four scenarios of closed area design, the simulated probability densities showed average proportions of time spent inside the closed area similar to the original proportions obtained with the 14 recaptured fish (Figure 5.4 top panels). Standard deviations (SD) of the simulated probability densities approximated 10% for the four closed area designs. The number of randomly sampled individuals was then changed to 7 and 21 to quantify the effects of the low number of recovered DSTs. Simulated probability densities revealed lower average proportions of time spent inside the closed area when only seven fish were randomly sampled (Figure 5.4 middle panels). Uncertainties in the estimated proportions increased as revealed by standard deviations of about 18%. Decrease in average proportions and increase in standard deviations occurred for the four closed area designs. Finally, when 21 fish were randomly sampled, the simulated average proportions of time spent inside the

four scenarios of closed areas were similar to the initially observed proportions (Figure 5.4 bottom panels). As expected, standard deviations decreased (SD = 9%) when 21 fish were sampled.

The second bootstrap analysis quantified the effects of inter-individual variability on the estimated closed area optimal spatial design. The 100 simulations of the spatial heuristic algorithm using 14 randomly sampled individuals suggested a 3723 ± 1622 km^2 (mean ± SD) area delimited by the following coordinates, 47°56'N - 48°43'N, 59°27'W - 60°02'W, as the average optimal spatial design for the fishery closed area (Figure 5.2b). This area is approximately 1000 km^2 smaller than the optimal area identified using the initial 14 tagged cod and approximately 1300 km^2 smaller than the original area. The simulated optimal area was located about 0°30' south of the original area.

The third bootstrap analysis, which quantified the effects of inter-individual variability on the closed area optimal temporal design, revealed an average optimal enforcement period of 64 ± 24 (mean ± SD) days from March 28th to May 31st (Figure 5.3b). This simulated optimal enforcement period was shifted by one day from the previously identified optimal enforcement period. The relatively high standard deviation of the simulated optimal enforcement period resulted mainly from uncertainties around the end date (SD of 7 days for start date and of 17 days for end date).

5.3.4. Conventional tagging experiments

Kernel density estimated from the 465 recaptures of the pre-collapse CT programs showed a multimodal distribution, with two principal modes (Figure 5.5a). The first mode was located in the northeast Gulf. The second mode was located along the slope of the Esquiman Channel, south of the closed area. Overall, the density function of the tagged population covered the entire west coast of Newfoundland. The kernel bandwidth equalled 0.61' in longitude and 1.11' in latitude. This difference in the two bandwidth parameters reflected the north to south distribution of the tagged population.

Kernel density estimated from the 345 recaptures of the post-collapse CT program showed a multimodal distribution with three principal modes (Figure 5.5b). In contrast with the distribution obtained for the pre-collapse period, the three modes were located along the southwest coast of Newfoundland. Indeed, the distribution mode observed in the northeast Gulf for the pre-collapse period was not observed during the post-collapse period. The first mode of the post-collapse distribution was located inside the closed area. The second was located south of the closed area, along slope of the Esquiman Channel, near the tip of the southwest coast of Newfoundland. The third mode was located south of Newfoundland, in NAFO division 3Pn. The kernel bandwidth equalled 0.64' in longitude and 0.94' in latitude. Again, this difference in the two bandwidth parameters reflected the north to south distribution of the tagged population, although it was less pronounced than during the pre-collapse period.

Differences in the pre- and post-collapse density functions resulted in lower proportion of the pre-collapse density function encompassed by the closed area (~3% difference, Table 5.2). Changes in the closed area design affected the encompassed proportions of pre- and post-collapse density functions. Spatial changes increased the encompassed proportions by 90% and 57% for the pre- and post-collapse periods. Temporal changes increased the encompassed proportions by 15% and 11%. The highest encompassed proportions were obtained for the two periods when both spatial and temporal changes in the closed area design were considered. These proportions however remained relatively low (~20%, Table 5.2).

5.4. Discussion

Effectiveness of fishery closed areas to protect fish spawning aggregation depends partially upon the movement rate of mature individuals across closed area boundaries (Murawski et al., 2000). This study demonstrates how the extent of adult fish movements across fishery closed area boundaries can be quantified from electronic tagging data. In our case study, reconstructed migration routes of individual fish equipped with data-storage tags revealed that Atlantic cod from the northern Gulf of St. Lawrence arrived in the fishery closed area in late March to early April, started to leave in late May, and spent on average 28.8% of their time within the closed area during its enforcement period. Using probability distribution functions of fish daily location, a simple algorithm was

developed to seek out the closed area size and location that maximized the proportion of time that free-ranging fish spent within the area relative to its size. This optimal spatial design was obtained with the displacement of the closed area south along the 200-m isobath, and a 4.5% decrease in the closed area size. Similarly, a second algorithm was developed to seek out the optimal closed area enforcement period from probability distribution functions of fish daily location. Results indicated that a reduced enforcement period from March 27th to May 28th would maximize the protection afforded by the closed area relative to the number of enforced days. The methodology developed here has important implications for the management of exploited fish populations. Indeed, finding the optimal design of fishery closures is crucial as excessively large and prolonged closures may diminish harvesters' compliance with regulations and increase enforcement costs, while too small and short closures may not offer sufficient protection to spawning populations. Both the spatial and temporal algorithms assume that times and areas are of equal conservative value. However, after modification of its design, the area may protect less the spawning aggregation and protect pre- or post-spawning aggregations instead. To decrease that risk, temporal and spatial constraints imposed on the two algorithms were chosen with respect to previous knowledge on spawning timing and distribution of Gulf cod.

Inherent limitations of ET experiments need to be considered when redesigning fishery closed areas. The quality of results from ET experiments depends upon the availability and accuracy of geolocation models used to estimate the probability

distribution function of fish locations, which in turns depends upon the nature of the environmental variables recorded by electronic tags with respect to the study species and oceanographic environment. While light-based or tidal-based geolocation are preferable if available, geolocation based on depth, temperature, and / or salinity may prove reliable when pronounced gradients are present (Andersen et al., 2007). The relatively pronounced bathymetry and bottom temperature gradients in the Gulf of St. Lawrence were key to the reconstruction of cod migration routes in our study. The geolocation model could be further improved by considering temperature data from all depth intervals across the water column (Galbraith et al., 2012). It would however increase computational time and complexity.

A second limit in ET experiments is the traditionally low number of tagged individuals due to high costs of tracking devices, which often precludes extrapolation to the population. Inter-individual variability can induce bias in estimated mean arrival and departure dates, and estimated average proportion of time that a population spent inside a closed area, especially if the number of recovered tags is low, and if some individuals deviate strongly from the general population pattern (Bolle et al., 2005). Using a bootstrap analysis, we showed that inter-individual variability induced a 10% uncertainty in the average proportion of time spent inside the original closed area. Expectedly, changing the number of randomly sampled fish showed that, as the number of randomly sampled fish decreased, the uncertainty around estimated average proportions increased (16% when 7 fish were sampled, and 8% when 21 fish were sampled). This result

underlines the relative sensitivity of ET experiments to the number of recovered tags. Interestingly, for the four scenarios of fishery closed area design, the simulated average proportions of time spent inside the various areas remained close to the initially observed proportions.

Bootstrap analyses were also performed to quantify uncertainties associated with the spatial and temporal changes in the closed area design suggested by the two heuristic algorithms. The 100 simulations of the spatial algorithm confirmed that the closed area should be displaced about 0°30' south for an improved performance. As well as this, the 1000 simulations of the temporal algorithm supported the suggested reduction of the enforcement period. However, inter-individual variability in timing of migration resulted in a high uncertainty around the end date of the simulated optimal enforcement periods (SD of 17 days). Indeed, some Atlantic cod departed from the closed area in May while other departed in June. Maturity analyses and ichthyoplankton surveys revealed that spawning in the nGSL Atlantic cod population continues in June in the area (Ouellet et al., 1997; Méthot et al., 2005). Reducing the enforcement period will thus increase risk of disturbance on the reproductive activity, as could displacing the area south if cod does not spawn south of the closed area. This issue exemplifies the trade-offs between optimal and maximal protection and underlines the need for careful consideration of uncertainties and of the knowledge on reproduction timing and location before modification of closure regulations.

An interesting aspect of inter-individual variability in movement is that the presence of alternative migratory behaviours within a population affects population stability, resilience, and productivity (Kerr et al., 2010), and may also affect effectiveness of fishery closed areas. Continuous observations provided by electronic tags allow the distinction of sedentary individuals from migratory individuals that exhibit homing behaviour. The population studied here comprises a mixture of sedentary and migratory individuals (Le Bris et al., 2013a). Keeping in mind that only three individuals were identified as resident in this dataset, none of the resident cod visited the closed area. Migratory fish, on the other hand, spent on average 36.6% of their time inside the original closed area. This result suggests that alternative migratory behaviours within a population can lead to disproportional levels of protection afforded by a fishery closed area depending upon the migratory behaviour type and the design of the fishery closed area. Rolling seasonal fishery closures provide an alternative for the spatial management of fish populations with complex structure (Armstrong et al., 2013). For instance, one could think of implementing a second seasonal fishery closure that would follow in time the closure studied here and target the area were resident fish were identified (i.e. Bonne bay area).

The proportion of population distributional range encompassed by closed area is another factor that impacts effectiveness (Claudet et al., 2008). The larger number of conventional tag recaptures, relatively to ET recaptures, facilitated broad-scale characterization of the adult population distribution during the fishery closed area

enforcement period, although during years preceding its establishment. In this study, kernel density estimations from CT data showed that low proportions of the tagged population density functions were encompassed by the closed area (9.8 and 13.4% for the pre- and post-collapse periods). Interestingly, these proportions increased to about 20% when the spatial and temporal designs of the fishery closed area were modified as suggested by the ET data. CT data thus supported results from the two heuristic algorithms, and confirmed that improved protection can be achieved with precise placement of targeted fishery closed area (Stefansson and Rosenberg, 2006).

Density-dependent habitat selection may induce changes in the proportion of the spawning population distributional range encompassed by a fishery closed area (Guénette et al., 1998; Grüss et al., 2011a). In this study, we had access to CT datasets from two periods of highly contrasted abundance levels. Kernel density estimations revealed a southeast contraction of the spring distributional range between the pre- and post-collapse periods. This distributional change was accompanied by a 3% increase in the encompassed density function. Previous studies have revealed that density-dependent effects partially govern local density in the nGSL population of Atlantic cod, and that the collapse of the population was accompanied by a southeast contraction in the population summer range (Tamdrari et al., 2010; 2012b). All together, these results suggest that the performance of a closed area located on the core of a population distribution increases as population abundance decreases. However, the observed change in distribution in our

study might also reflect the higher tagging effort placed in the 3Pn management division after the collapse (data not shown).

Finally, it is important to note that despite the observed increases in the encompassed proportions for both pre- and post-collapse population distributional ranges, resulting from with modifications in the closed area spatiotemporal design, these proportions remained at the lower end of the traditionally suggested 20-30% minimal levels of habitat protection required to ensure the persistence of heavily fished populations (Mangel, 2000; Gaines et al., 2010). CT data thus suggest that relatively small closed areas (~4000-5000 km^2) may not be effective in protecting wide-ranging migratory populations from commercial fishing. On the other hand, ET data indicated adequate levels of protection (from 29 to 51% depending on the design of the closed area). While CT and ET do not provide the same information, the large difference between encompassed distributional ranges and proportions of time spent inside the closed area by individual fish intrigues. Reasons for this difference are unclear and we can only speculate on potential factors. The temporal mismatch between the post-collapse CT and ET data (1995-2002 vs. 2007-2012) is unlikely to account for this difference as the population experienced an expansion of its distribution range since 2006 (Tamdrari et al., 2010; 2012b). On the contrary, that CT data tend to reflect more the fishery than the true population distribution, may partially account for the difference. In this study, CT recapture were corrected by catch data, which is unlikely to remove completely the effect of fishing effort on recapture distribution. Finally, some migratory behaviour (*e.g.*

resident fish in 3Pn) might be missing from the recovered group of fish equipped with DSTs, which could also account for the observed difference in protection levels. Indeed, the fact that DSTs depends on the fishery for the recovery may have induce a bias towards specific migratory behaviours.

5.5. Conclusion

Successful design of a closed area requires clear statement of the objectives and evaluation of the performance (Halpern and Warner, 2003). Our study did not attempt to evaluate the overall performance of fishery closed areas in terms of population persistence and fishery yield. It does not compare either the effectiveness of fishery closures to other management measures. Rather, this study demonstrated that ET and CT experiments provide complementary observations to address two factors that determine the level of performance of fishery closed areas on spawning grounds, namely adult movements across closed area boundaries, and the proportion of the spawning population density encompassed by a closed area. An inherent issue of ET experiments is the traditionally low number of recovered tags. However, with the lack of fishery data inside closed areas and the limited temporal coverage of scientific surveys, this study demonstrates that electronic tagging data offer a valuable solution to quantify individual usages of fishery closed areas by free-ranging fishes, and to redesign implemented fishery closed areas. Specific to our study system, results from both ET and CT experiments

suggested that the closed area designed to protect the spawning aggregation of Atlantic cod in the northern Gulf of St. Lawrence should be displaced south along the 200-m isobath. Provided the current miniaturization of electronic fish tagging technology continues, a similar methodology could be used to redesign fishery closed areas on fish nursery grounds. More generally, the methodology could be applied to any marine protected area.

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Tables

Table 5.1. Tagging and recapture information for the 14 Atlantic cod equipped with data-storage tags used in the study. T_{FL}: fork length at tagging. R_{FL}: fork length at recapture. M: migratory. S: sedentary.

Fish ID	Tag series	Tagging Date	Recapture Date	Days at liberty	T_{FL} (cm)	R_{FL} (cm)	% Time in closed area	Migratory behaviour
12996	LTD_1100	21/09/07	06/10/09	746	65	71	20.2	M
12998	LTD_1100	26/09/07	22/08/08	331	58	63	61.6	M
13012	LTD_1100	21/09/07	10/07/08	293	63	-	0	S
13036	LTD_1100	26/09/07	22/07/09	665	49	57	43.9	M
13039	LTD_1100	18/08/07	02/08/08	350	60	62	28.5	M
13363	LTD_1100	31/10/08	21/09/09	325	55	-	0	S
13380	LTD_1100	31/10/08	30/07/09	272	61	65	0	S
13388	LTD_1100	23/09/08	30/07/09	310	71	73	40.0	M
128	LTD_1400	07/11/08	26/10/10	718	53	56	13.3	M
423	LTD_1400	07/11/08	19/06/09	224	72	74	42.4	M
586	LTD_1400	31/10/08	14/10/09	348	53	-	71.6	M
2400	LTD_1400	03/08/11	06/07/12	338	58	63	27.3	M
2518	LTD_1400	03/08/11	15/11/12	470	62	-	28.4	M
2525	LTD_1400	19/10/11	06/09/12	323	71	73	25.8	M

Table 5.2. Proportion of tagged population density function (%) encompassed by the closed area for the two conventional tagging (CT) programs, and average proportion of time (%) spent by individual cod within the closed area for the electronic tagging (ET) experiments. Original area: Fishery closed area with original spatial design. Original duration: April 1st - June 15th. Optimal area: Spatial design that maximized the spatial performance index (see Section 5.2.3). Optimal duration: Enforcement period that maximized the temporal performance index (March 27th - May 24th).

Scenarios \ Tagging Experiment	Original area and original duration	Optimal area and original duration	Original area and optimal duration	Optimal area and optimal duration
Pre-collapse CT	9.8	18.7	11.3	20.1
Post-collapse CT	13.4	21.1	14.8	23
ET all (n=14)	28.8	38.2	35.9	50.3
ET migratory (n=11)	36.6	43. 4	40.8	57
ET sedentary (n=3)	0	0	0	0

Figures

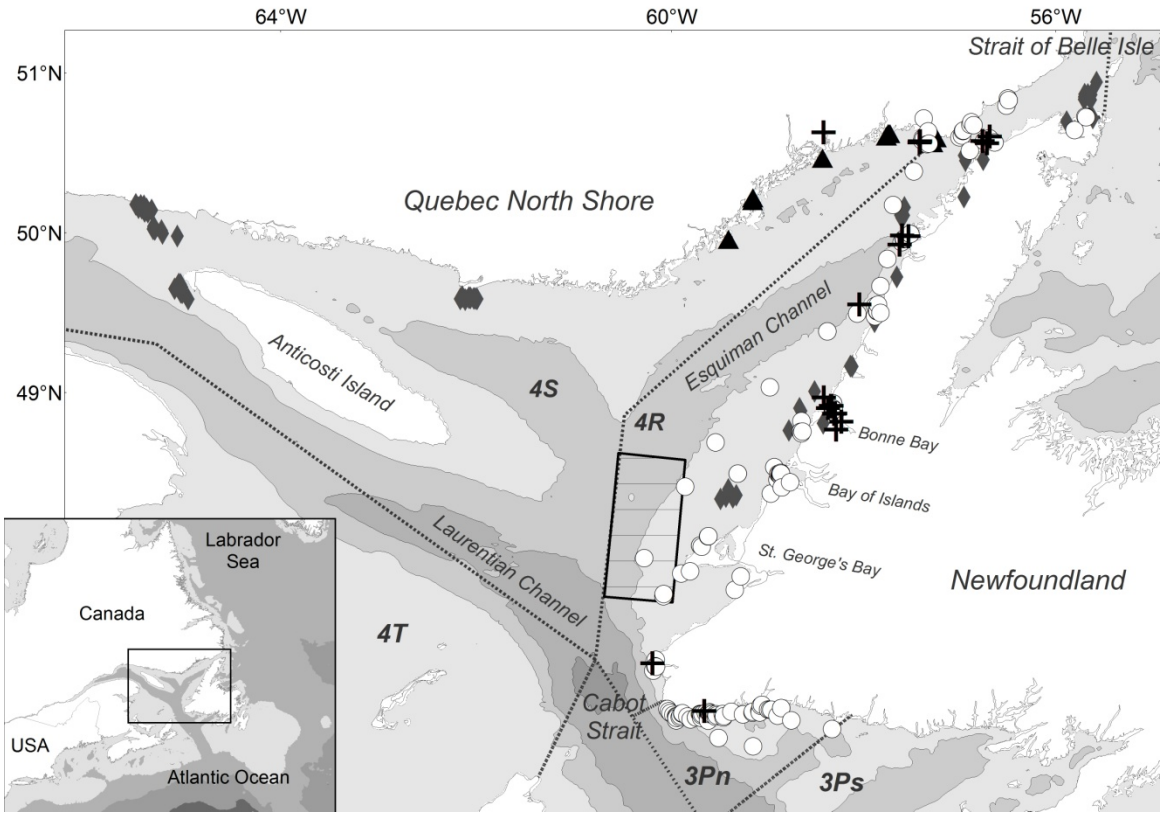

Figure 5.1. Map of the Gulf of St. Lawrence with tagging locations for all experiments. Black crosses: electronic tagging. White circles: post-collapse conventional tagging (Sentinel). Grey diamonds: pre-collapse conventional tagging (DFO). Black triangles: pre-collapse conventional tagging (MAPAQ). The hatched area shows the location of the fishery closed area. The dotted lines delimit the Northwest Atlantic Fisheries Organization management units. Grey contours on the main map represent the 200-, 400- and 500-m isobaths.

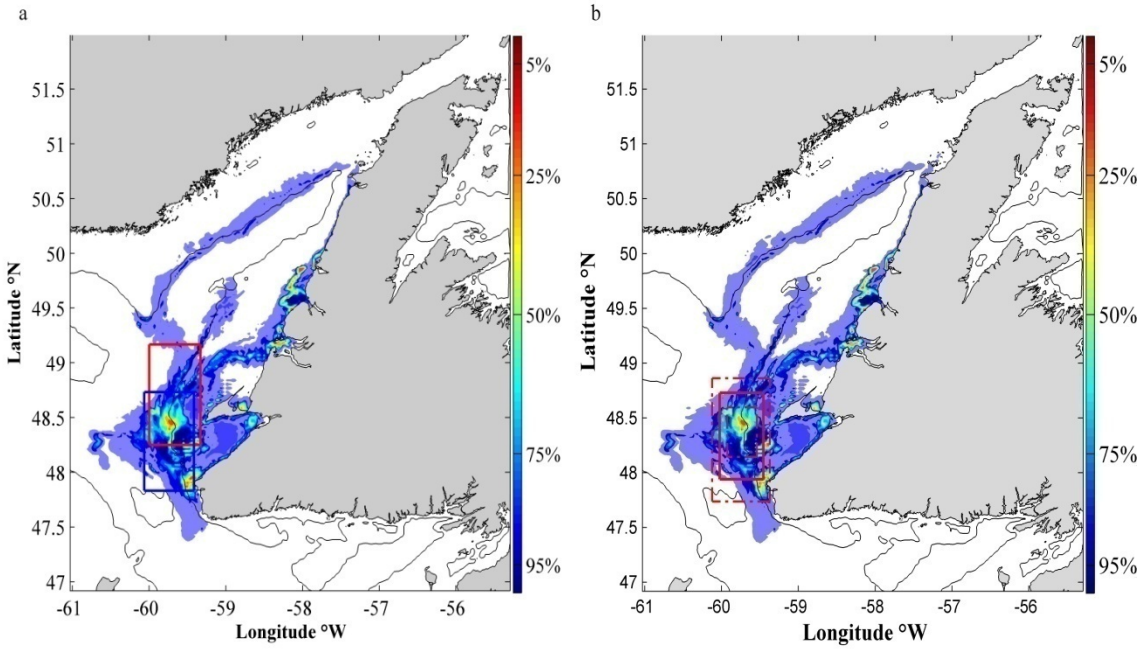

Figure 5.2. Average probability distribution function of the 14 Atlantic cod equipped with data-storage tags and tracked during the April 1st - June 15h period between 2007 and 2012. The thin black lines show the 200- and 500-m isobaths. The colour bar shows the proportion of time spent within coloured contours. a) The red box shows the original fishery closed area. The blue box shows the estimated optimal spatial design for the closed area. b) The solid red line shows the average optimal spatial design obtained from bootstrap analysis. The dotted red lines show the 95% confidence interval for the optimal spatial design obtained from bootstrap analysis.

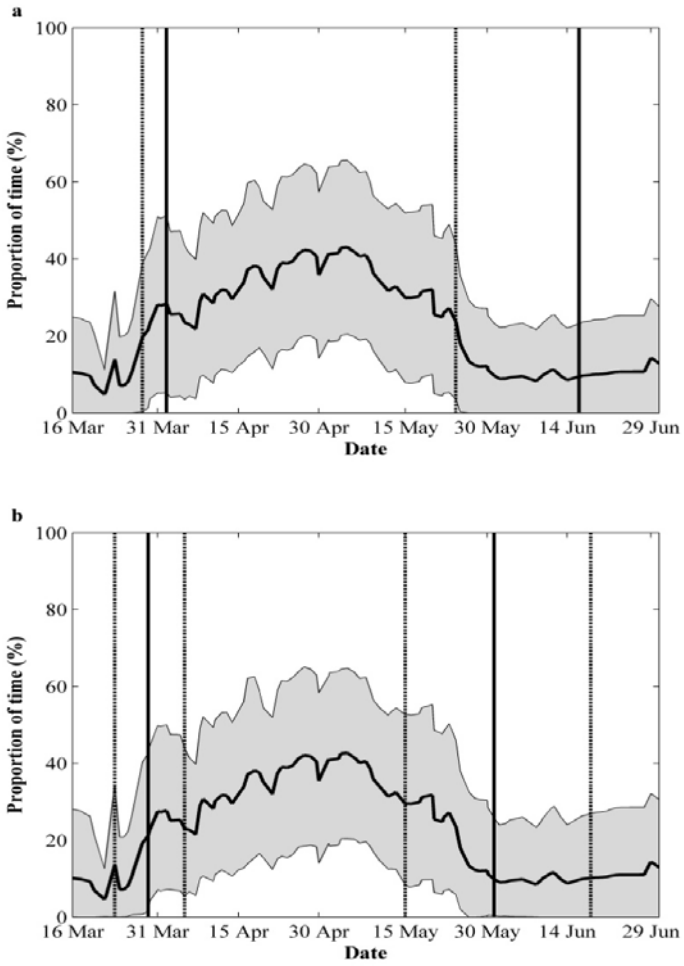

Figure 5.3. a) Average daily proportion of time that the 14 Atlantic cod equipped with data-storage tags spent inside the closed area. The shaded area shows the 95% confidence interval. The vertical solid lines delimit the original enforcement period (April 1st – June 15th). The vertical dotted lines delimit the estimated optimal enforcement period (March 27th – May 24th). b) Average daily proportion of time that the 1000 bootstrap samples of 14 Atlantic cod spent inside the closed area. The shaded area shows the 95% confidence interval. The vertical solid lines delimit the average optimal enforcement period obtained from bootstrap analysis. The vertical dotted lines delimit the standard deviation for the enforcement period start and end dates obtained from bootstrap analysis.

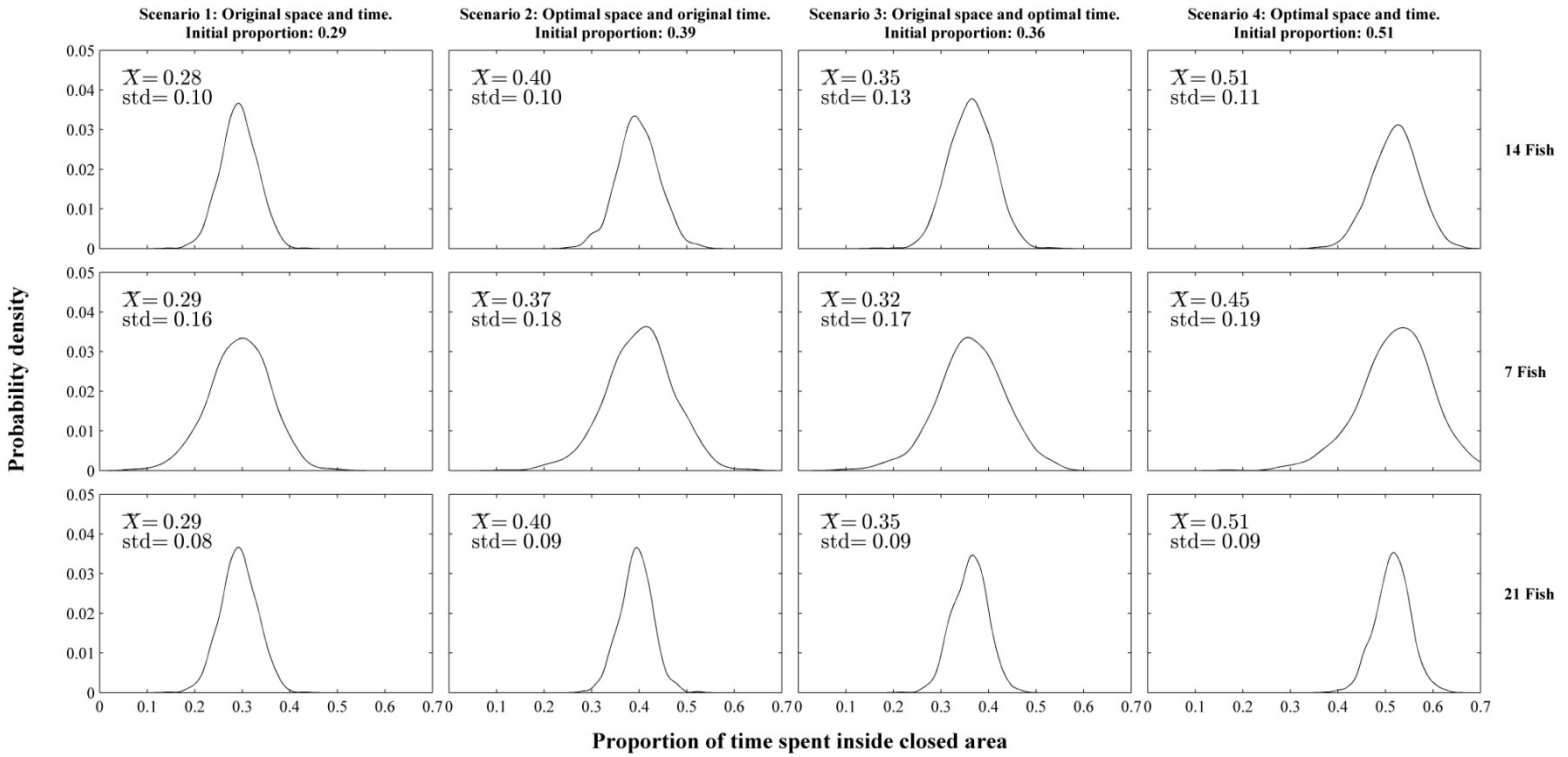

Figure 5.4. Probability densities obtained from bootstrap analysis for each of the four scenarios of fishery closed area design. Bootstrap analysis was performed by randomly sampling 1000 times 14, 7, and 21 fish from the original pool of 14 fish (see Section 5.2.4). Initial average proportions of time spent inside the closed area by the original group of 14 tagged fish are indicated for each scenario. $\bar{X}$ and std indicate the mean and standard deviation of the simulated probability densities.

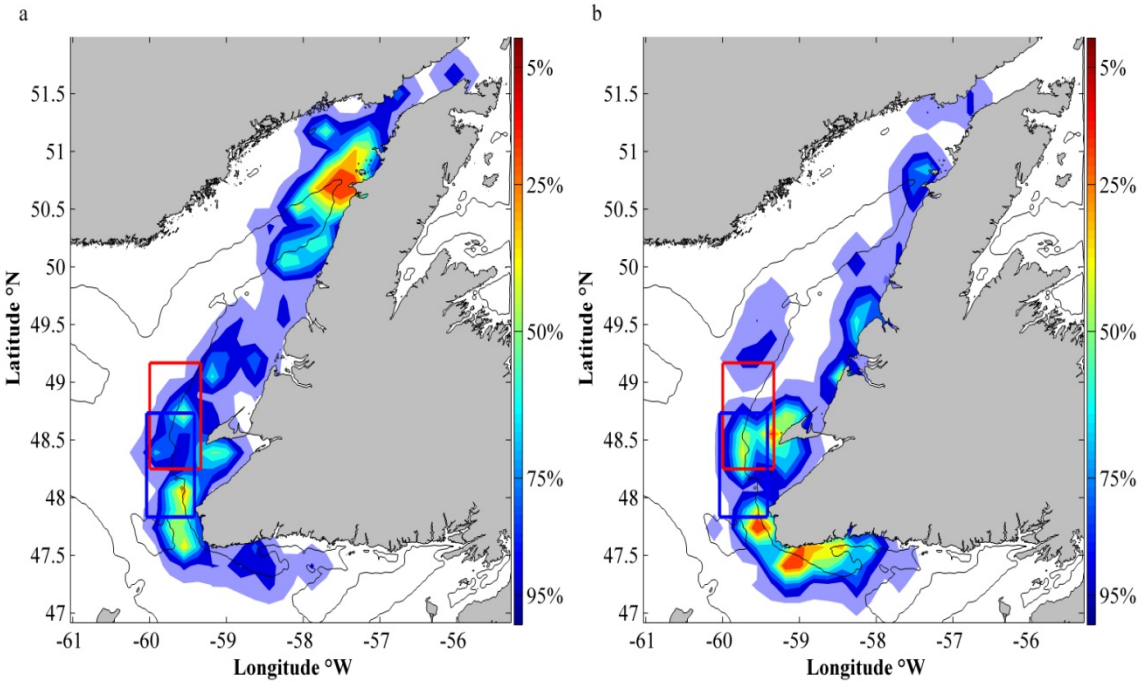

Figure 5.5. Tagged population density functions estimated from recapture positions of conventional tag during the April 1st - June 15th period. a) pre-collapse tagging experiment (1983-1985). b) post-collapse tagging experiment (1995-2002). The red box shows the original fishery closed area. The blue box shows the estimated optimal spatial design for the closed area. The thin black lines show the 200- and 500-m isobaths. The colour bar shows the proportion of density function encompassed by the coloured areas.

Chapter 6. Summary and Research Perspectives

The general objective of this thesis was to characterize individual variation in the migratory behaviour of Atlantic cod from the northern Gulf of St. Lawrence, and to assess the consequences of this variation on the structure and management of the population. Complete characterization of individual variation in migratory behaviour requires an understanding of the mechanisms that drive the evolution and maintenance of this variation. In chapter 2, I conducted a literature review to examine interplays between genetic, environmental, and social factors in shaping migratory behaviours of oceanodromous fishes. Evidence for fine-grained individual and population responses to environmental changes suggested that marine fishes are plastic in their migratory behaviours, not only in the timing, distance, and patterns of migration, but also in the propensity to migrate. However, whether this phenotypic plasticity is heritable and may lead to the evolution of migratory behaviour is unknown. Furthermore, the genetic basis and heritability of migratory traits have not been examined in any marine fish species. Future research is needed to partition the genetic, the environmental and the interactive (G × E interactions) components of the phenotypic variation observed in marine fish migratory behaviours. Such research could combine the tagging of small cohorts of known origin and the modelling of migratory traits using the 'animal model' (Wilson et al., 2010). Specific to Atlantic cod, I suggested that the environmental threshold model

provides a comprehensive theoretical approach to account for genotypic, environmental, and social factors in variation of cod migratory behaviour.

Chapter 3 focused on the population of Atlantic cod from the northern Gulf of St. Lawrence. An initial hypothesis was that the population comprises a mixture of resident and migratory individuals. The reconstruction of migratory routes of cod equipped with data-storage tags revealed individual variation in migration propensity within the population. Some individual exhibited extensive migration between wintering area in the relatively deep and warm waters of the Laurentian Channel, spring spawning area in the Esquiman Channel off the St. Georges' Bay, and summer feedings areas along the west coast Newfoundland. In contrast, other individuals exhibited yearlong residency in inshore waters along the west coast of Newfoundland. Furthermore, spectral analyses of depth distributions suggested a high variability in vertical migration patterns within and among migratory groups, a feature that appears common in Atlantic cod (Neat et al., 2006). The observed dichotomy in migration propensity adds to the mounting evidence of life-cycle diversity in populations of Atlantic cod (Smedbol and Wroblewski, 2002; Svedäng et al., 2007; Sherwood and Grabowski, 2010; Grabowski et al., 2011). I proposed two alternative hypotheses to explain the observed variation in migration propensity: the genetic determinism hypothesis and the partial migration hypothesis. The genetic determinism hypothesis suggests that the propensity of an individual to migrate is under genetic control and that variance in allelic frequencies maintains alternative migratory behaviours within a population or a population complex. The partial migration

hypothesis suggests that alternative migratory behaviours are maintained by a conditional strategy, in which the migratory behaviour adopted by an individual depends upon the environment and / or upon its developmental and social status. Which hypothesis prevails remains unclear. Interestingly, the publication of this research has stimulated the interest from geneticists to test for difference in gene expression at the *Pan* I locus between the migratory and resident individuals identified in this thesis. Preliminary results do not indicate concordance between allelic frequencies at the P*an* I locus and expression of migratory behaviour (Jean-Marie Sévigny, DFO Mont-Joli, pers. comm.).

The geolocation model used in chapter 3 demonstrated for the first time that demersal fish species can be tracked in the Gulf of St. Lawrence using electronic archival tags. In order to geolocate fish in the Gulf, I had to adapt existing models originally developed to track cod in the North Sea (Pedersen et al., 2008; Thygesen et al., 2009) and the Baltic Sea (Andersen et al., 2007; Neuenfeldt et al., 2007). I decided to use the statistical framework of the hidden Markov model developed by Pedersen et al. (2008) for its robustness and its flexibility. In contrast with the North Sea but similar to the Baltic Sea, the Gulf of St. Lawrence is characterized by a low tidal range that impeded the use of the tidal location method (Appendix B), and by relatively pronounced depth and temperature gradients. My choice of observational likelihood function (equation 3.2) within the hidden Markov model was therefore made to maximize the use of depth and bottom temperature gradients existing in the Gulf. Although no true model validation using simulated fish was performed (Neuenfeldt et al., 2007; Righton and Mills, 2008),

the inspection of the depth and temperature residuals suggested that the model performed well.

Several modifications to the model could improve its accuracy. First, a simple diffusion equation was chosen to model fish movement (equation 3.1). Using a more complex equation such as a correlated random walk, which include speed and angle of fish movement (Royer et al., 2005), could help refine estimations of fish daily location, but it would also increase the number of states to be estimated within the hidden Markov model and thus significantly increase the model complexity for relatively minor benefits. A second improvement to the model could consist in incorporating several depth and temperature data-point in the observational likelihood for each track day. For instance, instead of using exclusively daily maximum depth and associated temperature, daily maximum, minimum, and median depth with associated temperatures could be used to estimate the likelihood of a position. Again, this would further increase computational time and complexity.

The methodology used to detect periodicities in the vertical behaviour of Atlantic cod was unique. Several time-series analysis methods have been used to detect periodicities in the vertical migration of demersal and pelagic fish species, including analyses in the time domain (*e.g.* autocorrelation function; Neat et al., 2006) and in the frequency domain (*e.g.* spectral analyses; Stensholt, 2001; Shepard et al., 2006). In this study, the combination of polynomial regressions with spectral analyses using the fast

Fourier transform and a Hanning window allowed for rigorous and efficient detection of periodicities in the vertical movement of Atlantic cod. As the use of animal tracking technologies is rocketing worldwide, such straightforward and efficient algorithms are necessary to process the high-resolution datasets obtained from electronic tags.

Chapter 3 revealed year-round residency and a homing behaviour by adult cod to Bonne Bay area. I therefore assessed in chapter 4 the abundance of adult cod in Bonne Bay and examined the hypothesis that the bay harbours a local population of Atlantic cod. Data from a nearshore fish fauna survey and fisheries data revealed that adult cod are not abundant in the Bonne Bay. Yearly presence of juvenile and adult cod, evidence of summer spawning and fall juvenile settlement, and the length-at-age of juvenile cod, indicated that local recruitment occurs in Bonne Bay. The lack of genetic distinction between cod in Bonne Bay and in the Gulf indicated; however, that external sources of recruitment are substantial. The degree of connectivity between Bonne Bay and the Gulf is uncertain due to a limited knowledge on the dispersal patterns of early life stages. Indeed, no study has been conducted on the advection of pelagic juveniles from the Gulf into Bonne Bay, and more generally on dispersal of pelagic stages of Atlantic cod in the Gulf. Future research could include the development of a coupled biophysical model that simulates eggs and larvae transport patterns using the three-dimensional circulation model available in the Gulf of St. Lawrence (Saucier et al., 2003) along with temperature with prey-availability fields.

In spite of some research efforts, scarcely anything was known about the distribution of age-0 juvenile cod in the northern Gulf of St. Lawrence prior to this thesis. Yearly presence of age-0 juvenile cod in June in Bonne Bay indicated that Bonne Bay is a nursery area for Atlantic cod. Analysis of juvenile abundance indicated that no habitat supported a higher abundance of age-0 juvenile cod than other habitats within the Bay. Bonne Bay nearshore habitats are diverse and all have some level of structural complexity. This result underlines the need for local stewardship efforts to preserve structural complexity of the nearhsore habitats in Bonne Bay. Such efforts could help rebuild the northern Gulf of St. Lawrence cod population, which has suffered from low recruitment rates since its collapse (Chassot et al., 2009).

The last objective of this thesis was to quantify the effects of variation in migratory behaviour and population density distribution on the performance of fishery closed areas (chapter 5). First, I used the probability distribution functions of fish daily location estimated with the geolocation model developed in chapter 3 to quantify the fine-scale usage of a seasonal closed area by free-ranging individuals. Results revealed that the presence of alternative migratory behaviours within a population can lead to disproportional levels of protection between migratory groups, and underlined the need to consider alternative migratory behaviours in spatial management plans. Indeed, generalized management plans overlooking complex migration patterns may compromise population sustainability (Ruzzante et al., 2006). Rolling seasonal fishery closures may provide a management solution to protect alternative migratory behaviours. For instance,

a second fishery closure could be implemented. It would be located in area where resident individuals were identified (*i.e.* Bonne Bay and its vicinity), and its enforcement period would follow the spring spawning closure already in place off Bay St. George's (from June 15th to July 30th for instance). Second, I used conventional tagging data from two periods of contrasting abundance levels (pre- and post-population collapse) to estimate the proportion of the population density distribution encompassed by the closed area. Results supported the idea that when a closed area is located on the core of the population density distribution, density-dependence changes in population distribution increase the efficacy of fishery closed areas (Guénette et al., 1998).

Finding the optimal design of closed areas facilitates the sustainable management of fisheries resources by balancing immediate economic loss, enforcements costs, and protection of exploited populations (FAO, 2011). In order to find the optimal design (*i.e.* location, size, and enforcement period) of a seasonal closed area, I developed in chapter 5 two simple algorithms based on the probability distribution functions of the daily position of electronically tagged fish. Then, I performed bootstrap analyses to quantify uncertainties in the results induced by sample size and inter-individual variability. Application of the methodology to the closed area designed to protect the main spawning aggregation of cod in the nGSL indicated that a displacement south and a reduction of the enforcement period would increase the efficiency of the closed area. Interestingly, conventional tagging data supported this result. I believe that the methodology developed in chapter 5 could be used worldwide to refine the spatiotemporal design of existing

closed areas and to test scenarios for the implementation of new closed areas, whether they are fishery closures or marine protected areas.

In chapter 5, I supplemented electronic tagging data with conventional tagging data to refine location of fishery closed area. Electronic and conventional tagging data have been recently combined in Bayesian state-space models to estimate the transatlantic movement and exploitation rates of Atlantic bluefin tuna (*Thunnus thynnus*; Kurota et al., 2009) and fishing and natural mortality rates of Pacific Bluefin tuna (*Thunnus orientalis;* Whitlock et al., 2012). In the northern Gulf of St. Lawrence, a model that estimates the exploitation rate of the Atlantic cod population based on conventional tagging data has already been used (Le Bris et al., 2009). This model does not however consider the spatial structure of the population, and its accuracy is sensitive to initial conditions (*i.e.* initial mortality, tag loss and reporting rates). A sequential state-space model that combines archival and conventional tags to estimate movement and exploitation rates of the three management sub-units (3Pn, 4R, and 4S) could be developed. Such a model would be a valuable tool for the assessment of the stock. It can also be envisioned to integrate the conventional tags and pop-up satellite tags recently deployed in the 3Ps population in order to quantify mixing between the two management units (3Pn4RS and 3Ps).

To conclude, this thesis has made some theoretical progresses, it has developed new methodological approaches, and it has had direct management applications. First, it has provided increased evidence that the migratory behaviour of Atlantic cod in the

northern Gulf of St. Lawrence is more variable in both the horizontal and vertical planes than previously documented. Second, it has demonstrated that geolocation of demersal species is possible in the Gulf of St. Lawrence, an area of low tidal range. Third, it has demonstrated how to improve the design of fishery closed areas based on conventional and electronic tagging data. Finally, it has recommended to move the nGSL cod spring spawning closure south to increase its efficiency. This thesis has also raised questions about the mechanisms that maintain alternative migratory behaviours in population of marine fishes. It is now time to improve our knowledge on the mechanisms of variation in the migratory behaviour in marine fish species. Conditional strategies may well explain variation in migratory behaviour, not only for Atlantic cod, but also for numerous marine fish species.

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Appendix

Appendix A. State-space modeling.

State-space models (SSM) refer to a class of time-series methods developed to compute the optimal estimate of a hidden state given noisy observations. SSM constitute nowadays the most popular tool to analyze the tremendous amount of animal movement data collected by the increasingly small, affordable, and powerful animal tracking devices. The purpose of this appendix is to provide a general theoretical description of the state-space modeling framework, as the hidden Markov model used in Chapter 3 and 5 is one type of SSM, and another application of Bayesian SSM is suggested in the conclusion. Comprehensive reviews on the use of SSM for animal movement data are available in Patterson et al. (2008), Schick et al. (2008), and Jonsen et al. (2013).

Animal movement data are traditionally fitted with numerous dynamic models including the random walk and its derivatives (Morales et al., 2004), first passage time (Fauchald and Tveraa, 2003), fractal analysis (Turchin, 1996), and Lévy flight (Humphries et al., 2010). Although these models have proved helpful in modeling animal movement and behaviour, they do not consider errors that arise from the observation process (*e.g.* errors associated with Argos locations, light- or tidal-inferred locations). By combining these dynamic models, with statistical models that account for errors in the data acquisition process, SSM provide a rigorous and versatile statistical framework to model animal movement data.

The first component of an SSM is the dynamic model, which describes the biological process of interest (*i.e.* fish movement in this thesis):

$$\boldsymbol{x}_t = f(\boldsymbol{x}_{t-1}\,;\boldsymbol{\theta}) + \boldsymbol{\eta}_t \tag{A1}$$

where $f(\boldsymbol{x}_{t-1}\,;\boldsymbol{\theta})$ describes the evolution of the unobserved state $\boldsymbol{x}$ (*i.e.* fish position in this thesis), $\boldsymbol{\theta}$ is the unknown vector of parameters, and $\boldsymbol{\eta}_t$ is the process error associated with dynamic model. The second component of an SSM is the observation model, which refines state estimations from the dynamic model using available observations (*i.e.* depth and temperature in this thesis):

$$\boldsymbol{y}_t = g(\boldsymbol{x}_t\,;\boldsymbol{\theta}) + \boldsymbol{\varepsilon}_t \tag{A2}$$

where $g(\boldsymbol{x}_t\,;\boldsymbol{\theta})$ describes the relationship between the state $\boldsymbol{x}_t$ and the observations $\boldsymbol{y}_t$, and $\boldsymbol{\varepsilon}_t$ is the observation errors. Naturally, the choice of the dynamic and observation models depends upon the study species and the type and quality of data collected.

Solving equation (A1) and (A2) to obtain the probability density of the state $\boldsymbol{x}_t$ is done using a two-step recursive filter. Let $\boldsymbol{y}_{1:t}$ denotes the vector of all observations up to time t. The first step of the recursive filter (*i.e.* prediction step) computes the probability density of $\boldsymbol{x}_t$ given all previously available observations and fixed parameters $\boldsymbol{\theta}$ (omitted in equations A3 and A4 for clarity):

$$p(\boldsymbol{x}_t|\boldsymbol{y}_{1:t-1}) = \int p(\boldsymbol{x}_t|\boldsymbol{x}_{t-1})\, p(\boldsymbol{x}_{t-1}|\boldsymbol{y}_{1:t-1})\, d\,\boldsymbol{x}_{t-1} \quad \text{(A3)}$$

where the probability density $p(\boldsymbol{x}_{t-1}|\boldsymbol{y}_{1:t-1})$ is known from previous time step and the probability density $p(\boldsymbol{x}_t|\boldsymbol{x}_{t-1})$ is obtained by derivation of the transition equation (A1). The second step of the recursive filter (*i.e.* correction step) uses the Bayes' theorem to update state estimations with newly available observations $\boldsymbol{y}_t$:

$$p(\boldsymbol{x}_t \mid \boldsymbol{y}_{1:t}) = p(\boldsymbol{y}_t|\boldsymbol{x}_t)\, p(\boldsymbol{x}_t|\boldsymbol{y}_{1:t-1})\, / p(\boldsymbol{y}_t|\boldsymbol{y}_{1:t-1}) \quad \text{(A4)}$$

where probability density $p(\boldsymbol{y}_t|\boldsymbol{x}_t)$ is given by the observation equation (A2) and $p(\boldsymbol{y}_t|\boldsymbol{y}_{1:t-1})$ is a normalizing constant.

Two approaches are used for fitting SSMs to data (estimation of states and parameters): the frequentist approach using maximum likelihood estimation (MLE) methods, and the Bayesian approach. MLE methods are traditionally used with linear model and normally distributed process and observation errors. In such case, the Kalman filter provides the optimal algorithm to estimate states and parameters. When models are not linear and errors are not normally distributed, MLE methods can still be used but they require numerical integration across all possible states. If states are discrete, as in the hidden Markov model used in this thesis, the maximum likelihood estimations are performed by simply summing over all the discrete states (equation 5.4).

Bayesian methods are preferentially used with strongly non-linear and non-Gaussian models. States and parameters are considered as random values from predefined (prior) probability distribution functions. Then, Bayesian methods rely on simulations, typically using Markov Chain Monte Carlo (MCMC) techniques, to sample states and parameters from previous probability distribution functions until convergence towards the posterior distribution is reached. Bayesian methods are flexible and efficient, but also computationally intensive and require strong expertise.

Appendix B. Tidal location method (TLM).

The tidal-location method (Hunter et al., 2003a) was developed to track demersal fish species for which satellite-based or light-based geolocation methods are not appropriate. Developed and used to track European plaice (*Pleuronectes platessa*) in the North Sea (Metcalfe and Arnold, 1997; Hunter et al., 2003b), it has been used with thornback rays (*Raja clavata*) in the North Sea (Hunter et al., 2005; Hunter et al., 2006), and Atlantic cod in the North Sea (Neat et al., 2006; Svedäng et al., 2007; Pedersen et al., 2008) and the Gulf of Maine (Gröger et al., 2007).

As an exploratory work to the geolocation model used in chapter 3 and 5 of this thesis, I attempted to extract tidal information from the depth time-series recorded by DSTs to investigate whether the TLM could be used to track Atlantic cod in the GSL. Unfortunately, using the TLM in the GSL proved to be non-feasible. Here, I provide a description of my attempt to extract tidal information from depth time-series recorded by DSTs. This appendix illustrates the difficulty in using the TLM in areas with low tidal amplitude such as the GSL.

The core of the TLM consists in fitting sine-cosine waves to daily depth profiles recorded by the tag. Amplitude and phase of the fitted sine-cosine waves are then compared to predictions from a tidal oceanographic model of the study area in order to infer daily fish position. In the GSL, the major tidal constituent is the semi-diurnal M2 constituent, which period is $T = 12.4$ hours (Saucier et al., 2003). I therefore focused on

extracting the M2 tidal constituent from daily depth time-series recorded by the tag. The depth z at time t was modelled as follows:

$$z_t = \alpha \cos(\omega t) + \beta \sin(\omega t) + \varepsilon_t \quad \text{(B1)}$$

where $\omega = 2\pi / T$ is the angular frequency and ε is the error term. A linear least squares approach was used to solve equation (B1). Following Gröger et al. (2007), for each tracked day, equation (B1) was fitted twice to the depth time-series by sliding a 13 hour window. The first fit removed outliers (defined as data points outside the 95% confidence interval). The second fit was used to estimate tidal phase and amplitude. Daily amplitude and phase were calculated from the fitted sine-cosine wave with the highest goodness of fit (defined here by $gof = 1 + r^2 - rmse$, where r^2 is the coefficient of determination and $rmse$ is the root-mean-square error). The amplitude was given by $A = \sqrt{\alpha^2 + \beta^2}$ and the phase was given by $\theta = arcos(\alpha/A)/\omega$. Daily amplitude and phase were kept only if the model respected the following goodness of fit criteria: $r^2 > 0.75$ and rmse < 0.25 (Figure B1).

Two examples of cod equipped with DSTs are provided to illustrate the variability in the quality of tidal information extracted from recorded depth time-series. Cod #167 showed coherent results (Figure B2, left panel). The tag was programmed to record every 150 seconds. Comparison of estimated amplitude and phase (Table B1) with charts of co-amplitude and co-phase lines in the Gulf (Figure B3) suggests that cod #167 was located near Port-aux-Basques from 26 January to 28 January 2010. Interestingly, results from the

geolocation model also suggests that cod #167 was located along the southwest coast of Newfoundland during that period.

Cod #13380 however showed incoherent results (Figure B2, right panel). The tag was programmed to record every 30 minutes. Estimated amplitude showed two-fold variations from one day to the next (Figure B2 right panel, Table B1). Because of the low tidal range in the Gulf, such variations in amplitude would imply a movement of ~200 km from the Port-au-Port Peninsula to the Strait of Belle-Isle in a single day (Figure B3). This example, which is characteristic of most of the tagged cod in this thesis, clearly illustrates the difficulty in extracting reliable tidal information in the Gulf of St. Lawrence from depth time-series recorded by data-storage tags. It further illustrates how tag sampling frequency affects the performance of the TLM.

Table B1: Amplitude, phase, and goodness of fit statistics for cod #167 and #13380.

Fish ID	Date	Amplitude (cm)	Phase (°)	r^2	rmse
#167	26-Jan	24.7	53.8	0.78	0.12
	27-Jan	23.2	48.6	0.77	0.12
	28-Jan	30.6	53.6	0.80	0.12
#13380	31-Dec	74.2	15.5	0.92	0.16
	01-Jan	41.9	62.0	0.93	0.09
	02-Jan	69.5	45.4	0.91	0.16
	03-Jan	42.8	60.8	0.89	0.13

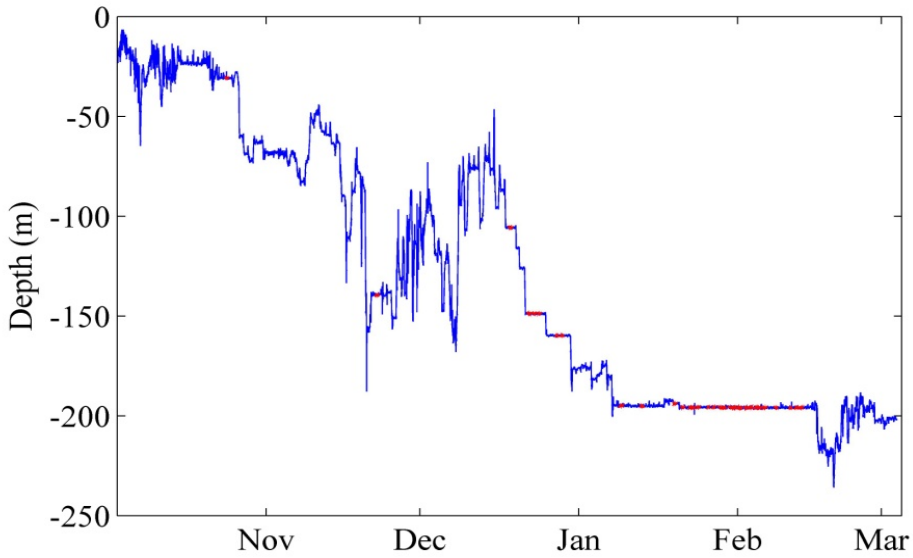


Figure B1: Depth profile recorded by tag #167. Red lines show the fitted sine-cosine waves that respected the following goodness of fit criteria: r^2>0.75, rmse<0.25.

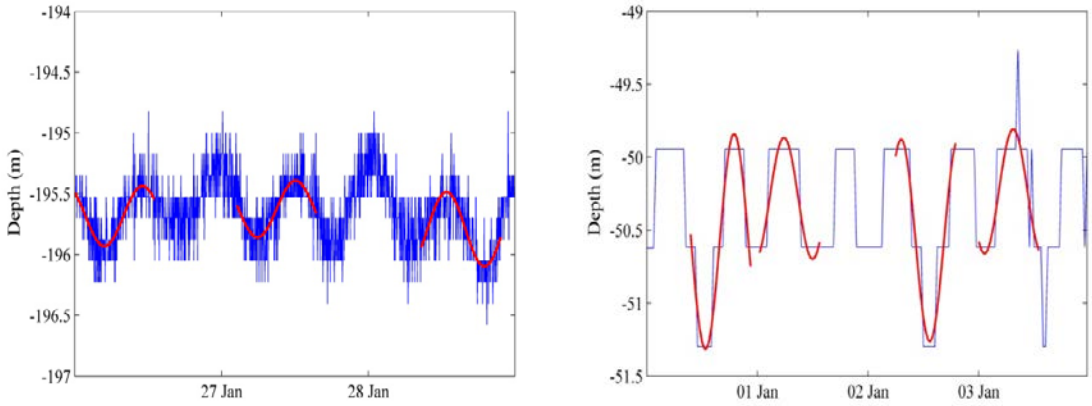


Figure B2. Depth time-series (blue) fitted with sine-cosine waves (red). Left: cod #167 from 26 January 2010 to 28 January 2010. The sampling interval is 150 seconds. Right: cod #13380 from 31 December 2008 to 4 January 2009. The sampling interval is 30 minutes.

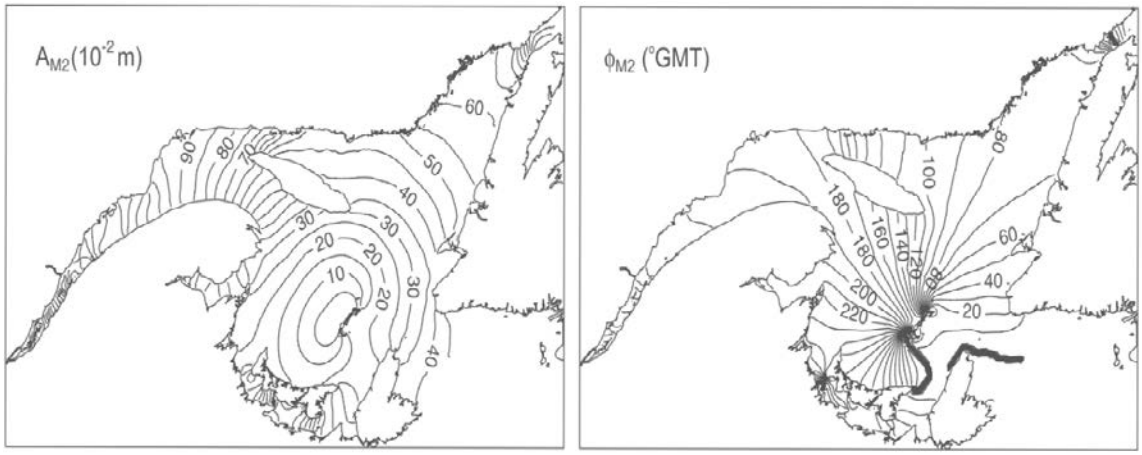
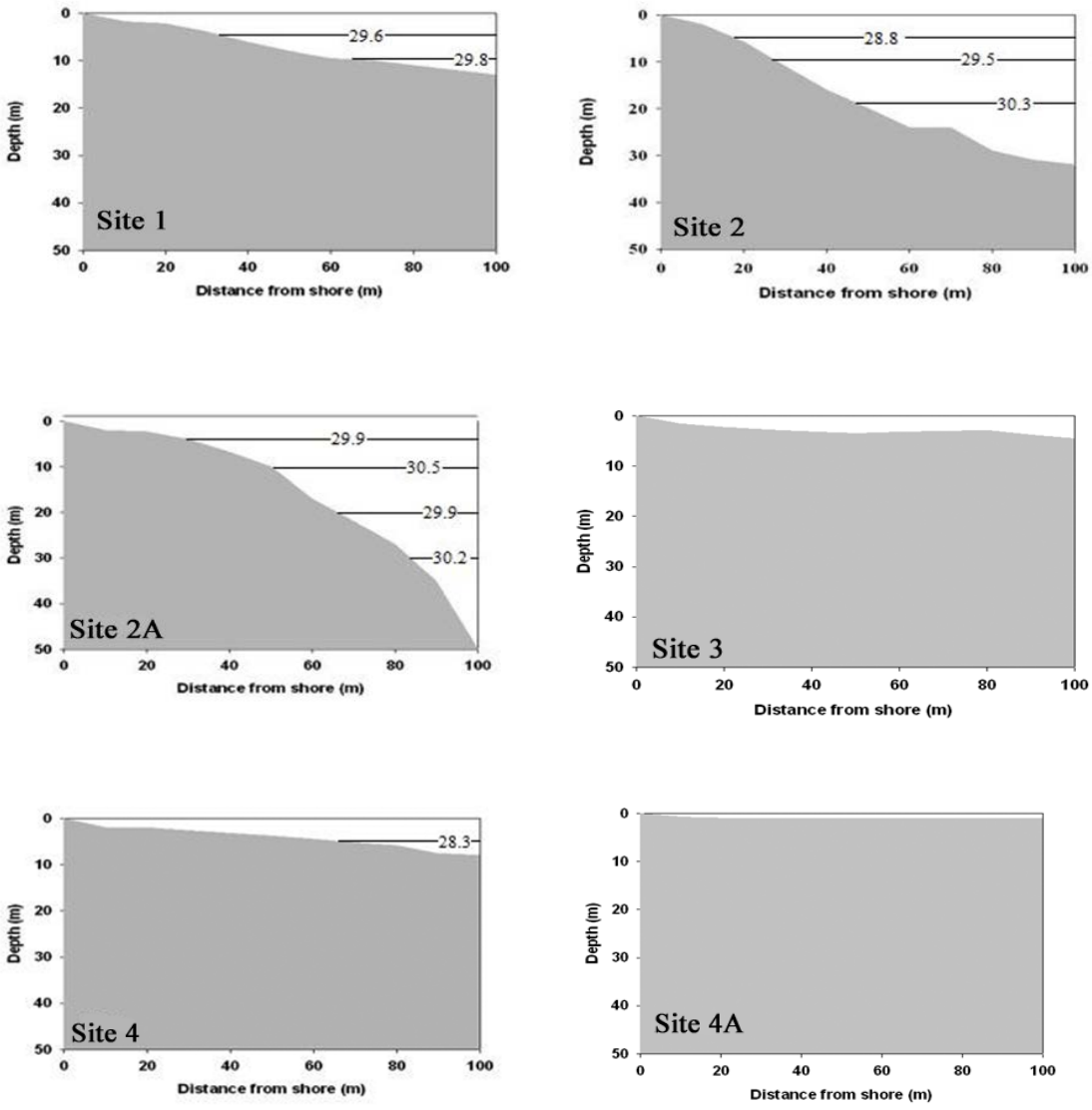


Figure B3. Charts of co-amplitude (A) and co-phase (θ) lines for the semidiurnal M2 tidal constituent in the Gulf of St. Lawrence (from Saucier et al., 2003).

Appendix C. Slope of the sea bottom and salinity (number within the plots) of the water column at six fish collection sites in Bonne Bay measured on 29 June 2009. Locations of collection sites are shown in figure (4.2). Near surface salinity at Site 3 was 20.8 and at Site 4A was 24.2. Not depicted is the shallow (< 2 m deep) barachois at Site 3A that had a near surface salinity of 1.8.



Appendix D. Depth (blue) and temperature (red) time-series extracted from data-storage tags. An original version of each dataset is held by the Department of Fisheries and Oceans Canada at the Maurice-Lamontagne Institute, Mont-Joli, Qc.

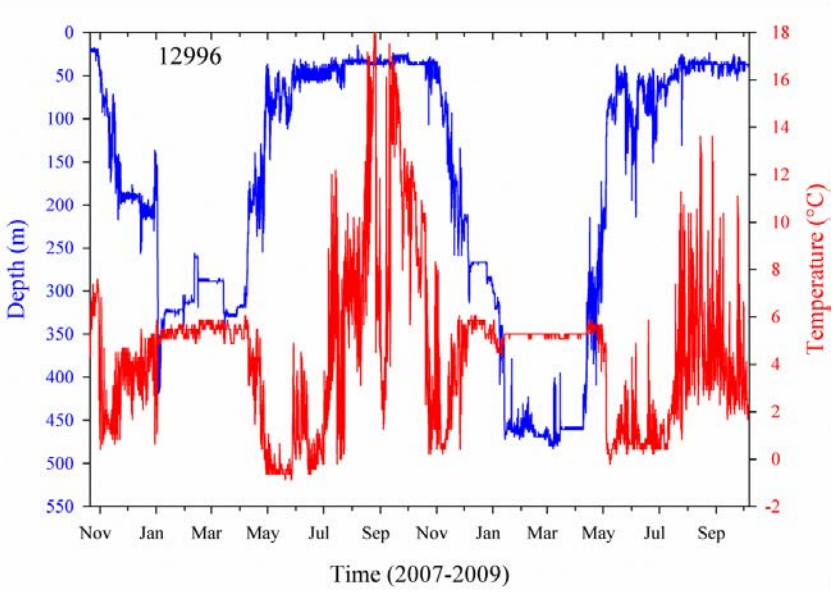


Figure D1. DST #12996. Series LAT1100. Tagging date: 9/21/2007. Recapture date: 10/6/2009. Recording duration: 746 days.

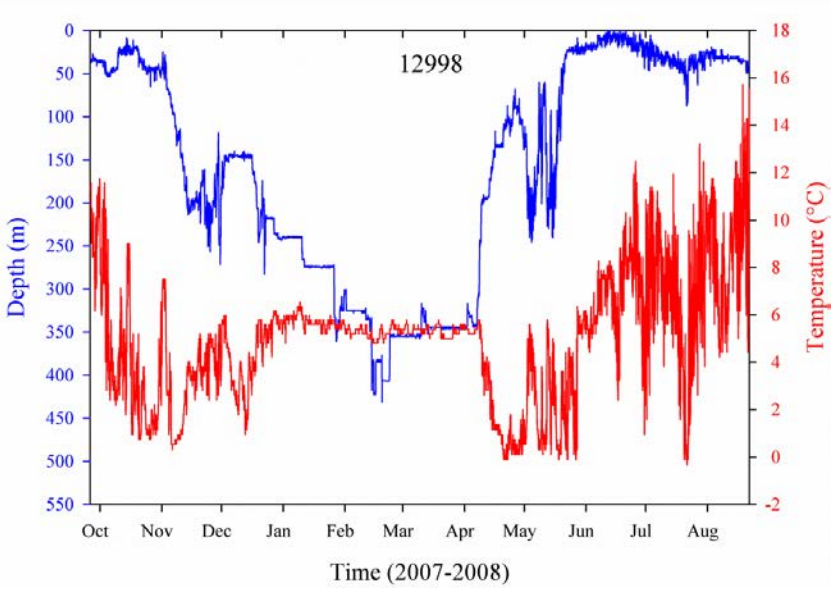


Figure D2. DST #12998. Series LAT1100. Tagging date: 9/26/2007. Recapture date: 8/22/2008. Recording duration: 331 days.

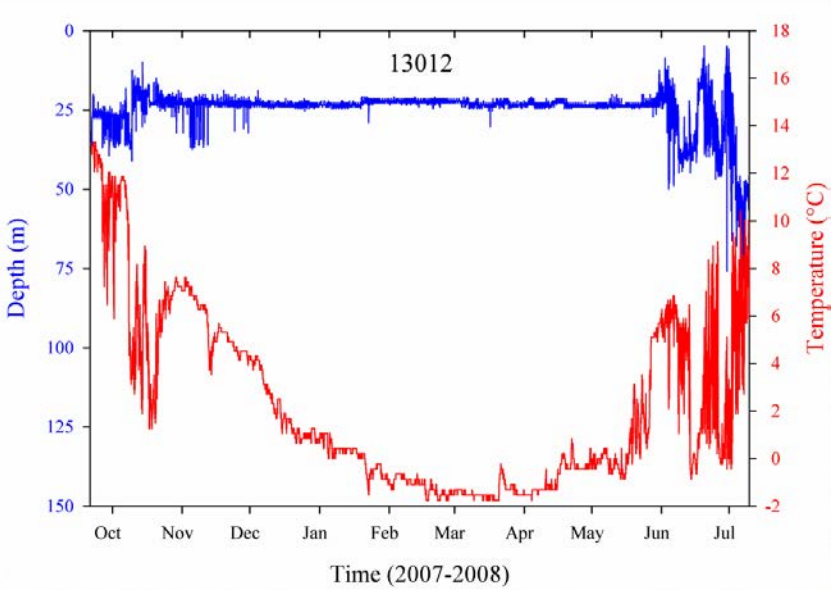


Figure D3. DST #13012. Series LAT1100. Tagging date: 9/21/2007. Recapture date: 7/10/2008. Recording duration: 293 days.

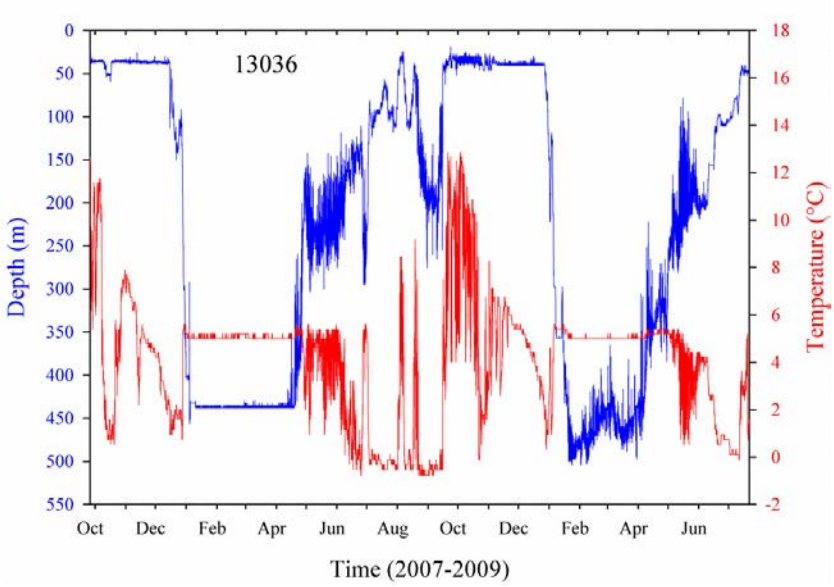


Figure D4. DST #13036. Series LAT1100. Tagging date: 9/26/2007. Recapture date: 7/22/2009. Recording duration: 665 days.

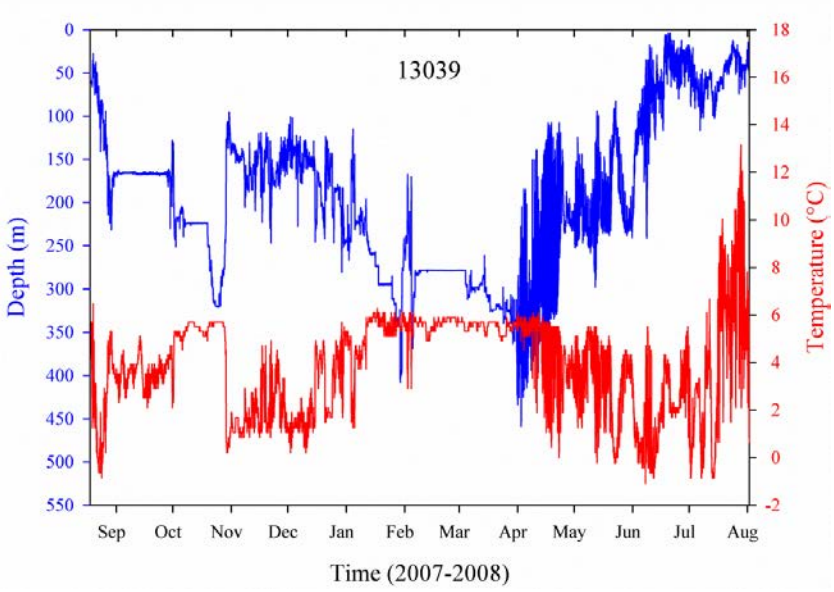


Figure D5. DST #13039. Series LAT1100. Tagging date: 8/18/2007. Recapture date: 8/2/2008. Recording duration: 350 days.

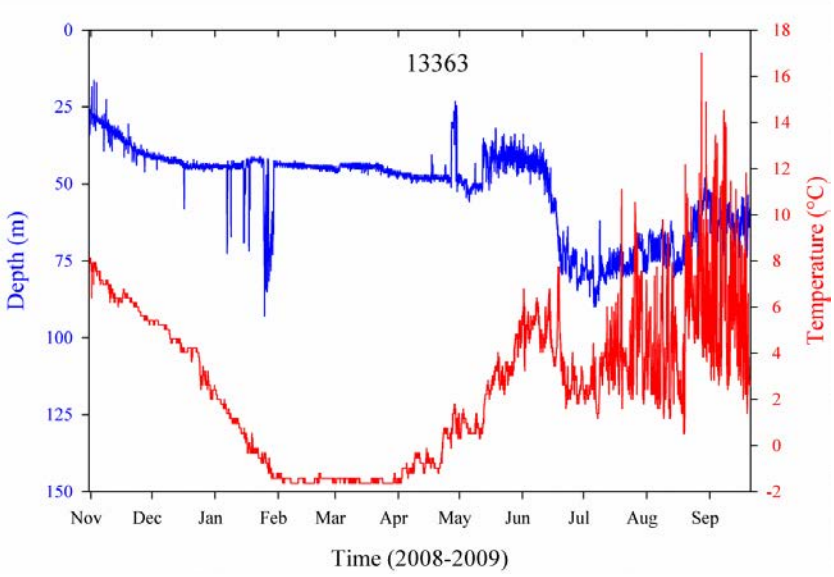


Figure D6. DST #13363. Series LAT1100. Tagging date: 10/31/2008. Recapture date: 9/21/2009. Recording duration: 325 days.

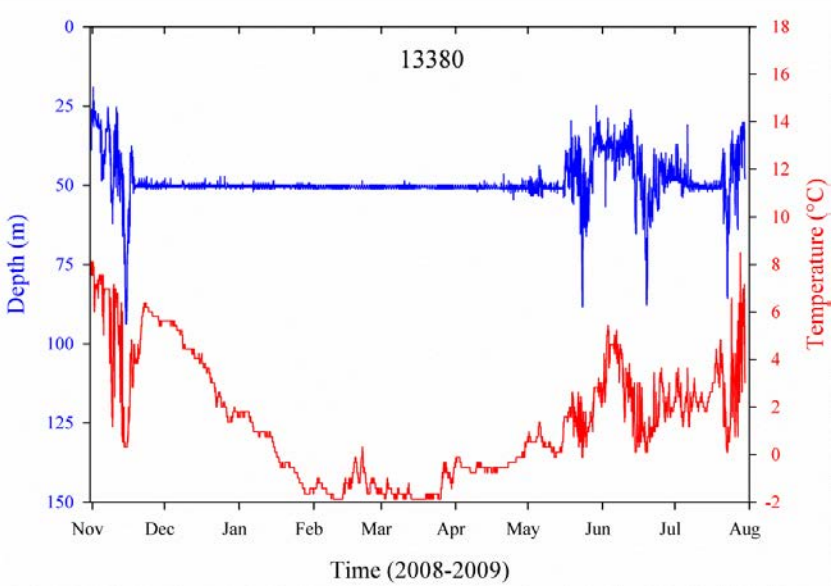


Figure D7. DST #13380. Series LAT1100. Tagging date: 10/31/2008. Recapture date: 7/30/2009. Recording duration: 272 days.

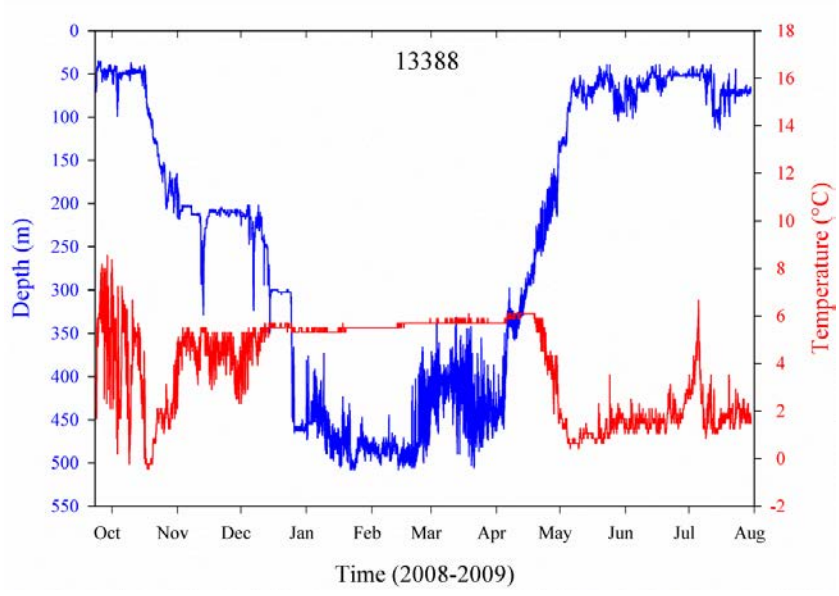


Figure D8. DST #13388. Series LAT1100. Tagging date: 9/23/2008. Recapture date: 7/30/2009. Recording duration: 310 days.

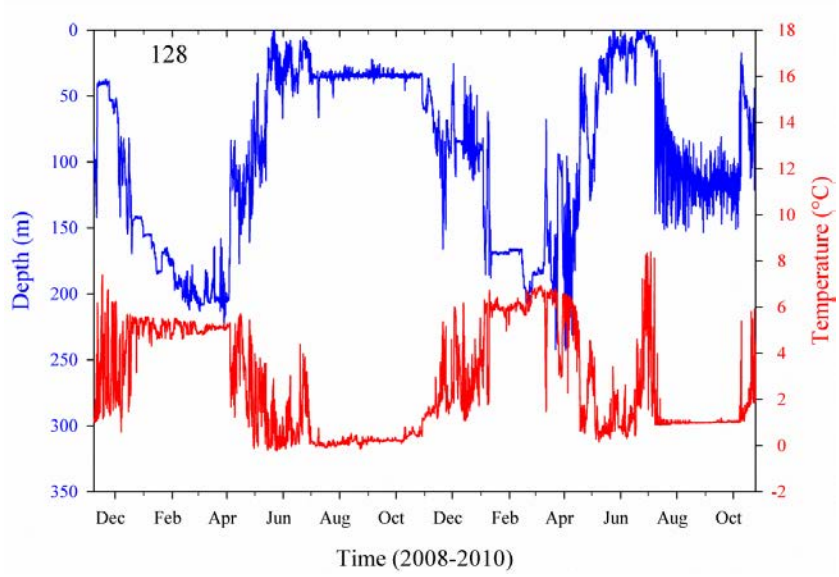


Figure D9. DST #128. Series LAT1400. Tagging date: 11/7/2008. Recapture date: 10/26/2010. Recording duration: 718 days.

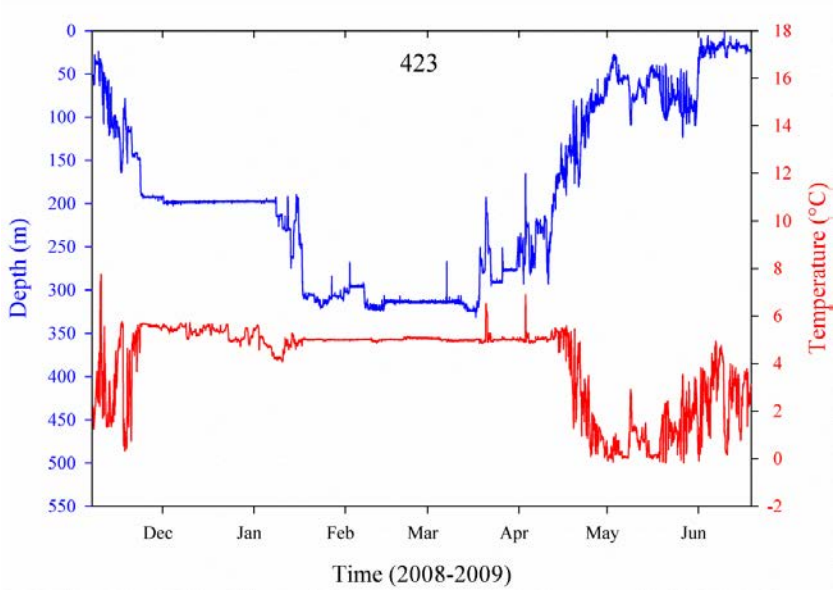


Figure D10. DST #12998. Series LAT1400. Tagging date: 11/7/2008. Recapture date: 6/19/2009. Recording duration: 224 days.

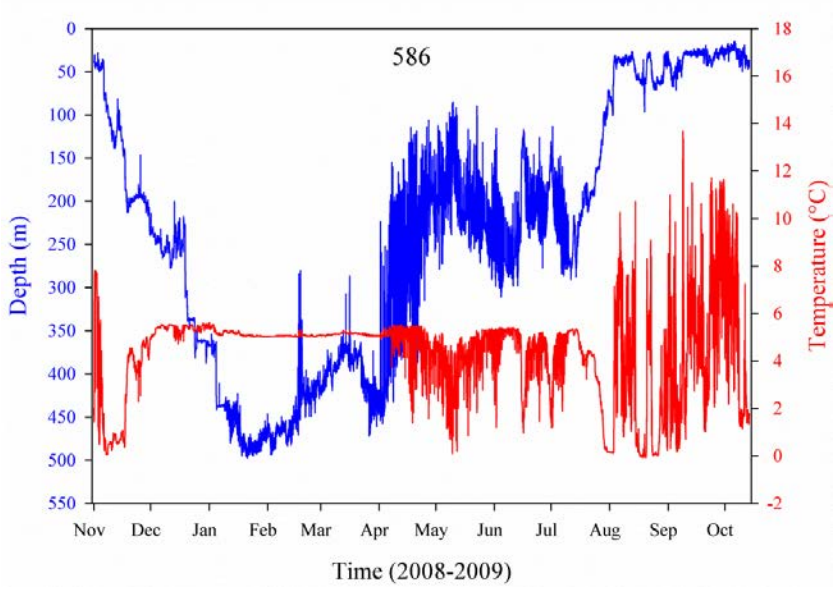


Figure D11. DST #12998. Series LAT1400. Tagging date: 10/31/2008. Recapture date: 10/14/2009. Recording duration: 348 days.

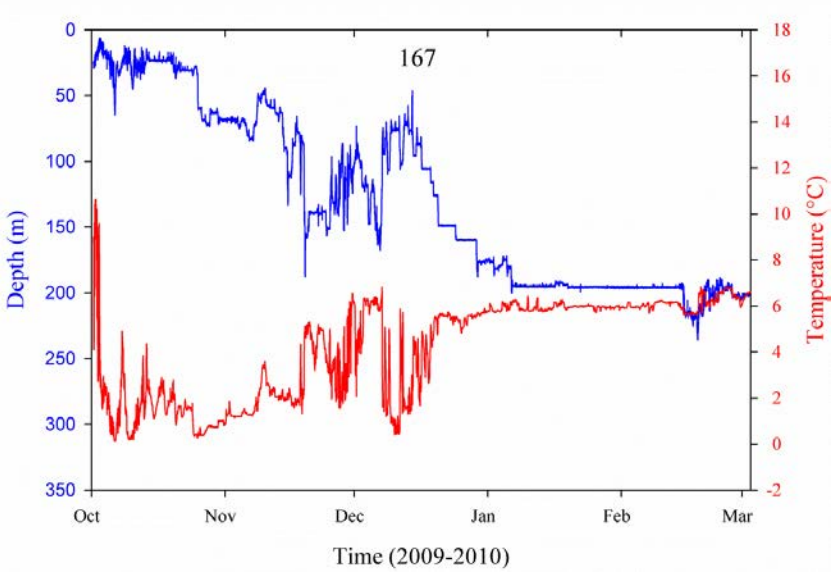


Figure D12. DST #167. Series LAT1500. Tagging date: 10/1/2009. Recapture date: 8/17/2010. End of recording: 3/3/2010. Recording duration: 153 days.

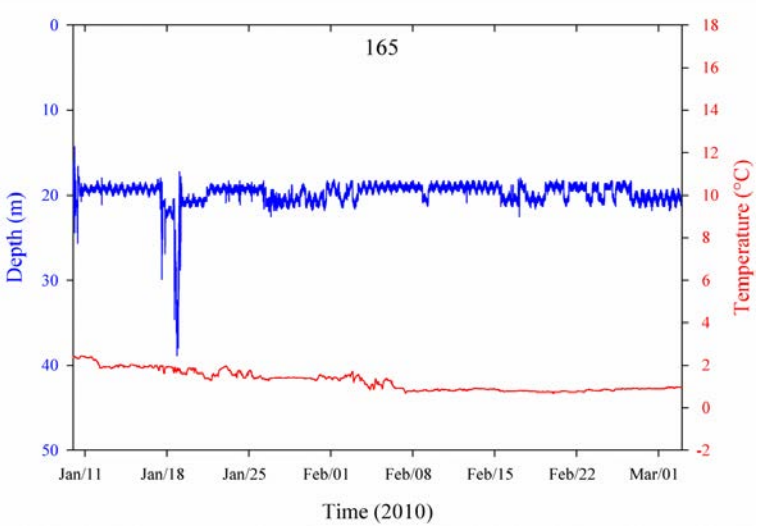


Figure D13. DST #165. Series LAT1500. Tagging date: 1/8/2010. Recapture date: 6/17/2011. End of recording: 3/3/2010. Recording duration: 54 days.

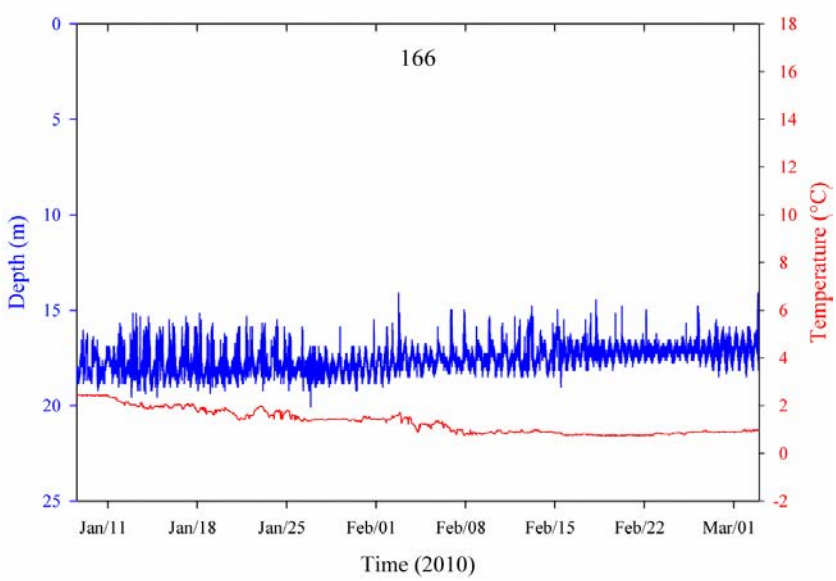


Figure D14. DST #166. Series LAT1500. Tagging date: 1/8/2010. Recapture date: 10/8/2010. End of recording: 3/3/2010. Recording duration: 54 days.

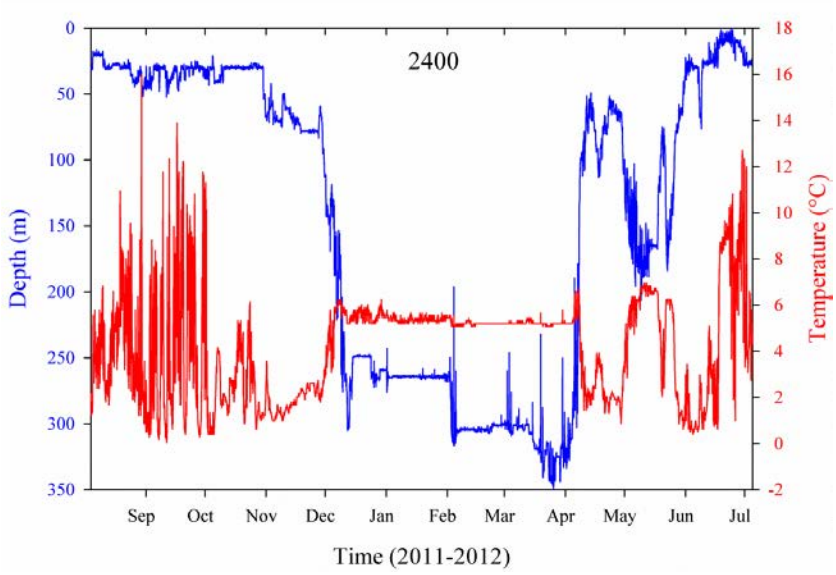


Figure D15. DST #2400. Series LAT1400. Tagging date: 8/3/2011. Recapture date: 7/6/2012. Recording duration: 338 days.

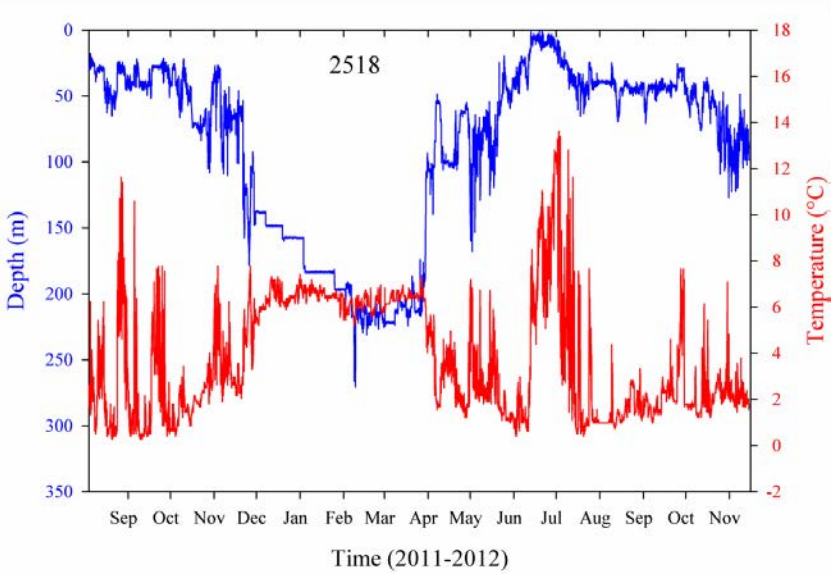


Figure D16. DST #2518. Series LAT1400. Tagging date: 8/3/2011. Recapture date: 11/15/2012. Recording duration: 470 days.

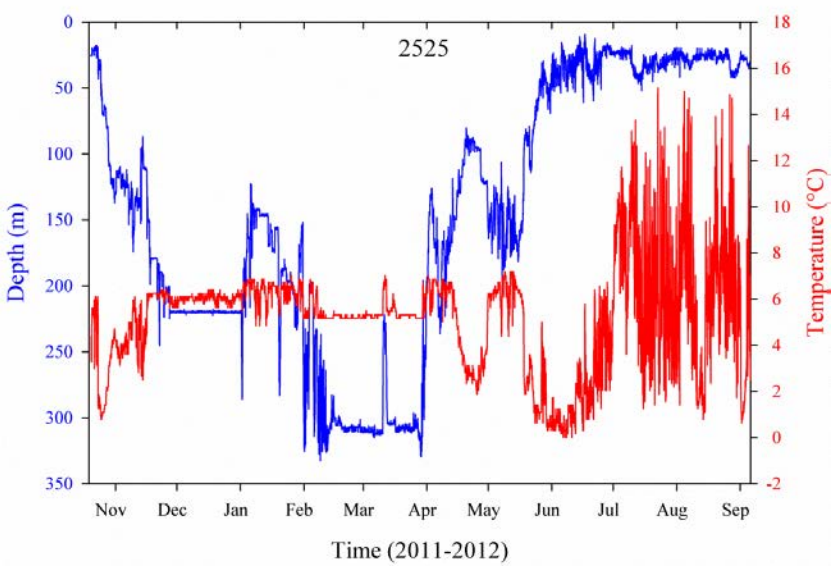


Figure D17. DST #2525. Series LAT1400. Tagging date: 10/19/2011. Recapture date: 9/6/2012. Recording duration: 323 days.